(pt 2)

143(p

Conseil Permanent International pour l'Exploration de la Mer

CHARLOTTENLUND SLOT – DANEMARK

LIBRARY
JUL 2 1965
FISH & WILDLIFE SERVICE

RAPPORTS ET PROCÈS-VERBAUX DES RÉUNIONS

Volume 143

Part II

CONTRIBUTIONS TO SPECIAL HERRING MEETINGS 1956

On Herring "Races"

En Commission chez

ANDR. FRED. HØST & FILS

COPENHAGUE

Prix: Kr. 30.00

Mars 1958

Conseil Permanent International pour
l'Exploration de la Mer
CHARLOTTENLUND SLOT – DANEMARK

RAPPORT
ET
PROCÈS-VERBAUX DES RÉUNIONS

Volume 143

Part II

ON HERRING "RACES"

En Commission chez
ANDR. FRED. HØST & FILS
COPENHAGUE

Prix: Kr. 30.00

Mars 1958

IMPRIMERIE BIANCO LUNO A/S
COPENHAGUE

Table of Contents

Opening Remarks and Note of the Convener, by A. Bückmann 5
Conclusions reached at Special Scientific Meeting on Herring "Races" held at Charlottenlund on 25.—27. September 1956 8

I. GENERAL PAPERS

1. The racial problem in herring from the viewpoint of recent physiological, evolutionary, and genetical theory, by J. H. S. Blaxter 10
2. The cranial osteology of the herring in racial investigations, by J. H. S. Blaxter 20
3. Counting of gill rakers as a method of morphological herring investigations, by Gerhard Krefft 22
4. Variation in meristic characters of young Atlantic menhaden, *Brevoortia tyrannus*, by Fred C. June 26

II. HERRING POPULATIONS OF THE NORTHERN ATLANTIC OCEAN

5. The tribes of the north coast herring of Iceland, with special reference to the period 1948—1955, by Á. Fridriksson 36
6. The Icelandic herring and racial problems, by H. Einarsson 45
7. Some considerations concerning the homogeneity of the Atlanto-Scandian herring, by O. J. Østvedt 53
8. Race formation and marine herring races. Biological premises, by Ju. Ju. Marty 60

III. HERRING POPULATIONS OF THE NORTHERN NORTH SEA AND ADJACENT WATERS

9. Race characters of the herring of the Clyde Estuary, by H. Wood (Summary) 65
10. Some remarks on methods used in herring "racial" investigations, with special reference to otolith studies, by B. B. Parrish and D. P. Sharman 66
11. The composition of the Minch herring stocks, by I. G. Baxter 81
12. Racial investigations on herring, especially adult herring in the Skagerak, by Aa. J. C. Jensen.. 95

IV. HERRING POPULATIONS OF BALTIC WATERS

13. Fecundity of Baltic herring, by R. Kändler and S. Dutt 99
14. Number of pectoral fin rays, by S. Dutt 109
15. The differentiation of biological groups of the herring in the southern Baltic, by J. Popiel ... 114

V. HERRING POPULATIONS OF THE SOUTHERN NORTH SEA

16. Some results of German investigations on herring larvae, by A. Bückmann and G. Hempel (Summary) 122
17. Meristic characters in the young herring of the Bløden Ground area, by K. Popp Madsen (Summary) 123
18. Stock composition of the young herring in the Bløden Ground area, by K. Popp Madsen (Summary) 124
19. The North Shields fishery, 1949—55, by A. C. Burd (Summary) 124
20. Selection of representative samples in a herring fishery, by I. D. Richardson (Summary) 125
21. Some changes in vertebral counts, by D. H. Cushing 126
22. On the distinction of herring races in the autumn- and winter-spawning herring of the southern North Sea and English Channel by means of the otoliths and an application of this method in tracing the offspring of the races along the continental coast of the North Sea, by K. H. Postuma and J. J. Zijlstra 130
23. On the spawning communities of the herring of the southern North Sea and the English Channel (preliminary results), by J. J. Zijlstra 134
24. Recherches sur la biologie du hareng, par Ch. Gilis 146
25. Considérations sur les harengs du sud de la Mer du Nord et de la Manche orientale. (Résumé d'observations faites de 1946 à 1955), par J. Ancellin 158

Opening Remarks and Note of the Convener

At the last annual meeting of the ICES a recommendation was passed by the Herring Committee that a Special Meeting be held concerning the problems of herring races. This Committee kindly suggested that I should convene this meeting, and my friend Mr. Parrish was selected as reporter. The Council's authorities complied with this recommendation, and I feel greatly honoured by their confidence and can only hope that I shall be able to justify it.

During the year the Herring Committee felt the necessity of an additional discussion of herring problems, with special reference to the causes of the decline of the herring fisheries in the Southern Bight of the North Sea. Of course the race question would form part of the evidence to be considered under that aspect. Therefore after some deliberations and correspondence the Bureau of the Council resolved that the meeting on the herring in the Southern Bight should be held in connexion with and immediately subsequent to the "race" meeting. It will be an important object of our race meeting to clear as much of the ground as possible for the deliberation of the Southern Bight meeting.

It is true that Heincke in one of his papers defined a herring race as a spawning community, the members of which were in a state of sexual intermingling, and which were distinguished from other communities by certain morphological features which were fixed by heredity.

We must however not press the expression of heredity. You are aware that Heincke started his work in the eighties of the last century, that is, well before the rediscovery of Mendel's work, and before genetics rose to the rank of a special branch of science. As a matter of fact Heincke did not doubt that the racial characters were in the first place formed by the conditions of the surroundings, but in conformity with the views of his age, Heincke assumed that in the course of time similar characters would get fixed hereditarily.

We must also realize that the problem Heincke was up against was much more generalized than our present problems. Heincke set out to test the question whether there was one large uniform stock of North Atlantic herrings, coming from the depths of the Northern Waters and surfing, as it were, against the different parts of the coast of northern Europe, attaining these coasts at different times of the year in order to spawn, giving origin at the same time to the different herring fisheries, and ebbing back once more into the northern deep.

To disprove this conception, Heincke showed that there were several forms of herring, which could be distinguished by certain morphologic features, and that herring shoals bearing a certain

stamp were to be found only in restricted areas. This he did by analysing rather small samples from different spawning places, in respect of a variety of characters.

In this context he would not have minded whether what he called the "racial" stamp of a community was inherited or if it was the stamp of the conditions of their environment, if only the stamp proved fairly constant, and so long as the members of the community could be identified by it.

By investigating as many characters as possible HEINCKE tried to get a rather comprehensive description and identification of the communities. He made certain that this remained fairly constant over a fair number of years in some instances; of course with his small samples he would not discover the minor fluctuations in the characters which we are aware of now.

Initially his intention was to get at a conjoint picture of all characters investigated. In his early publications, he gave combination tables of the actual values of many characters; however there were, and I suppose there are still, no satisfactory methods of forming an assessment of the co-variation of many characters. So HEINCKE was reduced to the comparison of the averages of the single characters and their errors, the method applied by practically all investigators up to the present.

Because of a criticism of C. G. JOHS. PETERSEN, HEINCKE dropped all those racial characters which were not individually constant, e.g., all body proportions. This may have been somewhat rash: We may well find out that the growth of herring is allometric only during larval development. There are some indications of this in HARDER's work. Later on additional characters were left out. These were the characters in which the influence of the milieu became soonest apparent or, in which mistakes in counts were easily made. There remained only the total number of vertebrae, and, partially, K_2. At present there is considerable evidence of plasticity also in these characters. Nevertheless subsequent workers used these characters, and additional characters are taken into account, which are known or suspected not to be individually constant, as the number of gill rakers, or of pectoral fin rays.

I must not prejudge the results of this meeting. Let me merely state two points:—

In the first place, HEINCKE was well aware of the fact that the herring was an instance of the splitting up of a species into several groups, an instance perhaps of formation of new species. By taxonomic investigations on quite different material, our knowledge has been greatly advanced about taxonomic questions. Therefore we must not take HEINCKE's view for granted, nor did HEINCKE intend to use his method for the discrimination between several self-contained stocks within the total range of the species. You will be aware that the conception of a self-contained stock did not arise until a considerable time after HEINCKE's herring papers had been published and stock statistics are a rather recent feature of our investigations.

The second point to which I wish to draw your attention is a freshwater parallel to our herring problems, i.e., systematics of Coregonids.

There may be as many as four different forms of large *Coregonus* within any one lake in Sweden or at the border of the Alps, differing in spawning time (between early autumn and late winter),

in spawning places (profundal, littoral, affluents, effluents), growth-rate, food, body proportions, and number of gill rakers. Every possible hypothesis has been formed: pooling everything in one species (Steinmann), dividing everything into four species on ecological grounds (Wagler), dividing everything in some 3 groups according to the number of gill rakers (Thienemann), describing lots of *Coregonus* sub-species different in each region (early workers).

In his excellent work Svärdson has recently shown that the number of gill rakers is strictly inherent, but that in small communities secluded by artificial implantation in lakes not inhabited by *Coregonus* certain genes may happen to be eliminated, which results in certain differences in the gill-raker variation of the new population as compared with the parental one.

Interbreeding may take place between different forms in a lake on a natural basis though at least in some instances the hybrid is not fertile.

By investigation of the chromosome sets Svärdson found strong evidence of the *Coregonus* groups being natural polyploids, with many irregularities in the chromosome partition system. This would account for the strong variability in *Coregonus* as well as for the fact that the mutants are not easily eliminated by lethal combinations.

With this state of affairs we cannot possibly know when, under what conditions, and in which waters the forms came into existence. It may not have been as early as the time when the now separated lakes were still connected with each other.

Let us, in our considerations, keep the possibility in mind, that rather similar conditions have led to the formation of the different local forms of the herring. There may have been a mutation in breeding time or the external conditions favoured for breeding, with the effect of practical sexual isolation, and rather a chance selection of genes and/or modifications.

We shall have further to consider the possibility, that there is no exact heredity of any numerical character, but the heredity of a reaction norm (Woltereck). This would mean that there might be a genotypic difference in the reaction on modifying influences *of the milieu* by the phenotypes.

In the following pages the communications delivered at the meeting are published according to the recommendation adopted by the Council at its final meeting. Abstracts are given of such papers as will appear in print elsewhere. The papers are arranged according to areas as in the discussion at the meeting. Some general papers have been taken together under one heading.

Most valuable information is contained in these papers, the discussion of which proved very fruitful. The issue will be found in the "Conclusions reached at the Special Scientific Meeting on Herring Races" compiled by the Reporter.

The meeting may be said to have been successful. Information given will help to form a more comprehensive and more correct picture of the life of herring populations in the North Atlantic area. The methods used for investigations have been scrutinized and criticized. A clearer knowledge is attained of the type of conclusions they will entitle us to make. Certain special problems emerged, the investigation of which is thought to be of special value at present. No more, I think, might rightly have been expected.

A. Bückmann

Conclusions Reached at Special Scientific Meeting on "Herring Races" held at Charlottenlund on 25.–27. September 1956

Convener: Professor A. Bückmann; Reporter: Mr. B. B. Parrish

Twenty-five papers, and a number of verbal communications, were presented at the meeting on a wide range of topics relating to herring "racial investigations". Of special importance among these were:—

I. The role of "racial investigations" in herring research.
II. Methods of investigation.
III. Present knowledge concerning the subdivision of the N.E. Atlantic herring population.
IV. Problems of taxonomic status of herring groups.
V. Future research requirements.

In the discussions which followed the presentation of the papers agreement was reached on a number of important issues relating to the above topics, and a series of conclusions were drawn up which the meeting wishes to bring to the attention of the Herring Committee. These are as follows:—

1. The primary objective of the field of study known as "racial investigations" is at present the identification and delimitation of "unit stocks", constituting distinct "management units", and determining the extent of overlap in time and space between them.

2. Concerning the methods which have proved useful in this work the following may be said.

(i) The meristic characters used by Heincke and later investigators as "race" characters exhibit plasticity under the influence of environmental factors, especially temperature, during the incubation period and early larval life. Therefore, though there may be genetic differences in these characters between the larger groups, the values of these characters cannot be regarded as genotypic.

In consequence, the meristic characters may be used as an indication of early life conditions, which can be of much value in studying the independence and mixing of herring of different origin. The greater the number of characters used the greater the prospect of confident discriminations being made. The following characters have been shown to be of use in this work:— Vert.S.; Vert. preah.; pectoral fin rays; K_2; gill-raker counts.

(ii) These meristic characters can only be used as "group" characters, but other characters afford information concerning differences in genotype and/or life history of individual fish. Most important of these are:—

(a) State of sexual maturity. This character gives a general clue to the spawning season of the adult age-groups, but available information tends to show that it must be used with caution as an index of the time of origin.
(b) Scale and otolith types. These reflect differences in the growth history and nature of the environment of individuals of different origin and habitat.

(iii) At present, it must be recognized that no single method is likely, by itself, to provide a means for separating quantitatively the members of different herring groups in areas of mixing. It is only by the application of several methods, including the direct methods, e.g., tagging and stock surveys, that accurate quantitative assessments are likely to be made.

3. In the light of published information and the data presented at this meeting it is recognized that a number of large groups of herring, separated by different spawning time, spawning locality and spawning conditions, and between which there is no

evidence of substantial interbreeding, can be enumerated. These groups are:—

(i) The herring living in open Atlantic waters and spawning off the Atlantic shores of northern Europe in late winter, spring, and perhaps early summer. These fish attain large size, and are characterized by mean Vert. S. of about 57·00 or greater.

(ii) The herring living in the North Sea, on the continental shelf to the west of the British Isles, and in the Transition Area and Baltic and spawning offshore between August and January. These herring attain a smaller size than the Atlantic group, and are characterized by mean Vert. S. between 56·0 and 57·0 in all but the Baltic area, where the values are less than 56·0.

(iii) The herring living in inshore waters of the North Sea, Transition Area, and Baltic and spawning during winter and spring in shallow waters. They are characterized by small size and Vert. S. generally between 55·0 and 55·5.

(iv) The Pacific herring, *Clupea pallasii*, which is represented in the north-eastern part of the ICES area. Herring of this group possess several features in common with the inshore winter—spring spawners defined under (iii).

Within each of these major groups, smaller communities or "tribes" may be recognized, differing in some degree in area of distribution, spawning time and/or locality and in one or more morphological and physiological characters. At present insufficient is known of the identities and degrees of interchange between these groups, and their further investigation constitutes the focus point for future research on herring "racial investigations".

4. Differences of opinion exist among herring workers as to the taxonomic status of the larger and smaller herring groups. It is desirable that agreement should be reached on this matter and that standardization of nomenclature should be achieved.

5. There is need of more extensive and intensive research on a number of items directly or indirectly related to the methodology and course of study in herring "racial investigations". The following research items are considered to warrant special attention by herring workers.

(i) Experimental work designed to establish with greater certainty than at present the relation between the values of meristic characters and environmental factors. The accomplishment of this task is dependent upon success in rearing herring in aquaria under controlled conditions.

(ii) Studies of the genetical constitution of herring groups. It is recognized that this work presents formidable problems, but attention is drawn to the proposal made by Professor A. C. Hardy in his address to the special meeting of the Herring Committee in Edinburgh in 1949, to the need for a special European centre of research into the genetics of fish.

(iii) Investigations of homing "instinct" in herring, and the physiological processes involved in the maturation cycle, with special reference to the endocrine systems involved.

(iv) Experimental work to determine the response of herring to external stimuli with a view to a better understanding of the factors influencing migration and the process of "navigation". It is recognized that this work is also largely dependent upon successful establishment of herring in aquaria.

(v) Intensive tagging of adult herring in spawning condition, and of adolescent herring before they leave the nursery grounds. The need for an intensive tagging programme on the Bløden nursery ground is of special importance.

(vi) Comparisons of otolith and scale types of herring within each main spawning group, and a study of the growth of the otolith nucleus during the larval and post-larval stages.

(vii) Intensive study of meristic and other characters of herring on all spawning grounds. It is recognized that this requires close cooperation between herring workers of different countries.

(viii) Investigations of the link between the herring stocks in the N.E. and the N.W. Atlantic.

(ix) Studies of stock and echo-sounder surveys, to determine the movements and change in composition of the fishable concentrations in different areas.

(x) Studies of fecundity of herring spawning in different areas.

Recommendation

At the close of the meeting a recommendation was passed that the papers presented at the meeting should be published in a special volume of the "Rapports et Procès-Verbaux".

1.

The Racial Problem in Herring from the Viewpoint of Recent Physiological, Evolutionary, and Genetical Theory

By J. H. S. Blaxter,
Marine Laboratory, Aberdeen

I. Introduction

The work of Heincke, Lea, Johansen, Lissner, Schnakenbeck, and many other scientists of European countries around the North Sea and Baltic has shown that the herring (*Clupea harengus* L.) may be divided into groups which are usually called "races".

Despite the volume of literature on this subject the question of herring "races" is still considered as a "problem". Agreement has not been reached on the actual number, or nature, of the "races". No one has shown how they originated, why they remain distinct and how they are related to each other. An understanding of the basic factors underlying the "races" would be of great value in interpreting the results of those racial investigations essential to the study of herring populations and their conservation. If in fact the population parameters are different in the "races" they will have to be considered separately from the point of view of conservation.

Apart from recent papers by Krefft (1954, 1955) there appears to be no contribution to this problem which takes into account the great strides forward which have taken place in the fields of evolutionary, genetical, physiological, and ecological theory and in their application to the study of systematics and taxonomy.

"Race" is a rather loose term embracing any subdivision of a species which is distinct in some way from another subdivision of the same species. It connotes a genetical distinction underlying the differences between these subdivisions. In any but marine environments races are usually geographically separated. In this paper the subdivisions will be called "groups" so that the reasoning may in no way be prejudiced.

The groups have been delimited so far by meristic, by other morphological, and by physiological characters. The first include counts of vertebrae, keeled scales, and fin rays and, more recently, gill rakers (Krefft, 1954). These characters are unsuitable for assigning individual fish to a group and can only be used by the statistical analysis of samples of fish. Morphological differences are found in the dermal bones of the cranium, in scales, otoliths, and body proportions, and physiological differences in growth-rate and spawning time. Differences in growth-rate will also be reflected in the scales and otoliths.

It is proposed to deal mainly with four groups of herring and to compare them as follows:—

Firstly { Atlanto-Scandian spring spawners
North Sea autumn spawners

Secondly { Scottish west coast (Minch) spring spawners
Scottish west coast (Minch) autumn spawners

The Norwegian spring spawners (Johansen, 1919; Lea, 1929; Runnström, 1936, 1941a) spawn in February and March off the west coast of Norway and along the northern and eastern edges of the North Sea shelf. These herring are about 29—30 cm. long at first spawning and may reach a length of 35 cm. or more. The mean vertebral count lies between 57·1 and 57·5 being lower in the more northerly spawners. The keeled scale count has a value of about 13·8—14·3.

The interrelationships of the North Sea autumn spawners have recently been discussed by Krefft *et al.* (1955) and Cushing (1955). In general (Johansen, 1924; Wood, 1932, 1936; Lissner, 1934; Hodgson, 1934) it may be said that they migrate

in an anticlockwise direction in the North Sea. The fish spawn on the banks off the Scottish coast in August and September, on the Dogger in September and October, and in the Southern Bight in November and December. They spawn for the first time at the end of their third or fourth years when about 24—26 cm. long. The maximum length attained is rarely more than 30 cm. The vertebral counts lie between 56·35 and 56·65, being somewhat higher in the south; the keeled scale counts lie between 14·5—15·1.

There are considerable differences in the life histories and characteristics of the two main groups described above and they are not usually found together. In the Minch, however, the spring and autumn spawning groups are less geographically distinct (Baxter, 1952, 1953, 1954, 1956 and unpublished data). The spring spawners spawn in February and March along the north-west coast of the Scottish mainland and on the continental shelf north-west of Lewis and near St. Kilda. The young spend some time in the Minch area and spawn at the end of their third year when about 27 cm. long. After first spawning the adults are only found in the Minch at or near the spawning season. The mean vertebral count is about 57·0 and keeled scale count 14·0 (Wood, 1932). The autumn spawners spawn in August and September in the North and South Minch fairly close to the shore and the young are found in the nursery grounds around the Minch, often mixed with young spring spawners. The autumn spawners also spawn for the first time at the end of their third year at a length of about 25 cm. They have a mean vertebral count of 56·4—56·5 and a keeled scale count of 14·6 (Wood, 1932).

II. Nature of Group Differences in Herring

a) Morphological characters

Spring and autumn spawned fish develop at different times of year and in different environmental conditions. Thus differences in the characters of the annual rings of the scales (Lea, 1929; Hodgson, 1950) and in the appearance of the centre and other features of the otolith (Einarsson, 1951; Parrish, 1954) may well be due to differences in the environment when these structures are laid down.

Differences in body proportions may be genotypic but there have been reports of environmental conditions disturbing allometric growth (Huxley, 1932; Martin, 1949). Differences in the opercular bones (Anon., 1938) and in the dentary (Blaxter, 1957 b) are small and it is difficult to ascribe their formation to any particular factor.

b) Meristic characters

Heincke (1898) and Schnakenbeck (1931) considered these to be inherited in the herring but Schmidt's (1917—21) work showed the importance of the environment in determining meristic characters in other fish. Johansen (1924) and Lissner (1934) applied such concepts to herring and since about 1936 (Davis, 1936) the modern viewpoint has been adopted which considers that there is a certain plasticity in the meristic characters due to environmental circumstances in early life. We may review here the work which leads to this conclusion.

The effect of environmental conditions on meristic characters has been studied in the Pacific herring, *Clupea pallasii*. Hubbs (1925) and Rounsefell (1930) found an increase in mean vertebral count northwards along the North American coast. Rounsefell and Dahlgren (1932) found a significant negative correlation between mean vertebral count and average air temperature during the spawning months in Prince William Sound. Tester (1937) found a similar negative correlation in Jap inlet over a period of seven years but not in other inlets, and also found a gradation in vertebral count with latitude. Tester (1938) showed a negative correlation between mean vertebral count and water temperature during the spawning season from 1926 to 1935 in Barkley Sound. Runnström (1933), working with *Clupea harengus*, showed that in 1931 the mean vertebral counts of 0-brood herring from different areas on the Norwegian coast were negatively correlated with the temperatures in these areas during March. Later Runnström (1941 a) showed a similar negative correlation among spring spawners from different regions in the north-east Atlantic. Bückmann (1950) found a negative correlation between mean vertebral count and temperature for autumn spawned herring larvae in the North Sea. Le Gall (1935) correlated K_2 counts in herring with temperature, and vertebral counts with salinity, but it seems doubtful whether the latter is valid.

It seems then that the number of vertebrae in a given species of fish developing in warm water is smaller than when developing in cold water, although some other meristic characters increase in number in warmer environments, as shown by Cox (1923) in the stickleback (*Apeltes quadracus*), Schmidt (1917, 1919) in the guppy (*Lebistes reticulatus*), and Schultz (1927) in *Notemigonus crysoleucas*.

Laboratory, hatchery, and transplantation experiments have confirmed most of the field results. Rearing experiments by Schmidt (1921) on the sea trout (*Salmo trutta trutta*), Dannevig (1932) on the cod (*Gadus morrhua*), Mottley (1937) on the Kamloops trout (*Salmo kamloops*), Gabriel (1944) on the killifish (*Fundulus heteroclitus*), Tåning (1944, 1952) on *Salmo trutta trutta*, and Dannevig (1950) on the plaice (*Pleuronectes platessa*) showed the dependence of vertebral count on temperature. Ege (1942) by transplantation experiments with the eel pout (*Zoarces*

viviparus) found that the pectoral fin rays were environmentally determined while Svärdson (1950, 1952), from similar experiments with the whitefish (*Coregonus*), concluded that scale counts were higher at lower temperatures.

Although herring have been reared to a stage where vertebral counts can be made (Meyer, 1878; Schach, 1939; Dannevig, 1948), the incubation temperature was not controlled. Hempel (1953) and Blaxter (1957), however found that myotome counts were higher in larvae reared at low temperatures. The latter found that myotome counts of some spring and autumn spawners do not differ significantly when the same rearing temperatures are used, and that myotome and vertebral counts are related.

Other environmental conditions may affect meristic characters, as shown in *Salmo trutta trutta* (Tåning, 1952) for oxygen and carbon dioxide tensions, and in the stickleback, *Gasterosteus aculeatus* (Heuts, 1949), and possibly *Zoarces viviparus* (Schmidt, 1920) for salinity.

Kyle (1923), Hubbs (1926), Schnakenbeck (1929), and in particular Gabriel (1944) have developed the theory that temperature affects the relations between processes controlling growth and differentiation so that low temperatures retard differentiation relatively more than growth. At low temperature, for instance, a greater amount of presumptive myotome tissue would be developed before segmentation; thus, greater size would be accompanied by more vertebrae. There is good evidence that larger fish (in any given age-group of a species) have more vertebrae, as shown generally by Huntsman (1919), and in *Clupea pallasii* by Tester (1937) and McHugh (1942).

Many meristic characters then are partly controlled by environmental factors during early development and growth. But there is also evidence for genetical factors playing their part in some fish, e.g., *Lebistes reticulatus* (Schmidt, 1917, 1919), *Zoarces viviparus* (Ege, 1942), *Fundulus heteroclitus* (Gabriel, 1944), *Gasterosteus aculeatus* (Heuts, 1947), *Coregonus* (Svärdson, 1950, 1952), and *Salmo trutta trutta* (Tåning, 1952). Work on the herring has not yet shown any genetical influence, and it is unlikely to do so until herring can be satisfactorily reared in reasonable numbers. Meanwhile, it seems possible that the various groups of herring in the Baltic and eastern North Sea, which have low vertebral counts of 55·5 to 56·0 (Johansen, 1924), are genotypically different from other groups.

c) Physiological characters

Growth. In the four groups considered in this report, the average length of spring spawners is greater than that of autumn spawners of the same age, where both are over three years old (e.g., Hjort, 1909; Baxter, unpubl.). Farran (1938) showed that the eggs of spring spawners were larger, and Friðriksson and Timmermann (1951) pointed out the wide range in size of eggs of different groups, the eggs being largest in the Atlanto-Scandian group. Schnakenbeck (1929) showed that spring spawned larvae were longer than those spawned in autumn. Blaxter (1956a) found from rearing experiments that the larvae of spring spawners were longer and heavier than those of autumn spawners when reared under similar conditions. Differences in egg and larval size may be of either genetical origin or a result of parental feeding before spawning but in the latter case one might expect spring spawners to have smaller eggs!

Growth can vary considerably in nearby localities (Tester, 1937), and it may be dependent on temperature (Andersson, 1947) as well as food, but where different groups are living together most of the year, size differences may indicate a genetical difference in growth-rate. For instance the Zuider Zee and Baltic spring spawning herring are very small and this may suggest a genetical difference in growth-rate compared with larger fish brought up in similar conditions, but we are quite ignorant about this.

So far, however, it has been impossible to demonstrate any genetical control of growth-rate, due to a wide variety of spawning times and nursery areas, and the fact that spring and autumn spawners do not live together sufficiently long for a controlled comparison to be made. The fact that autumn spawners are generally smaller, age for age, than spring spawners, is probably partially explained by the growth checks associated with spawning, which is earlier in autumn spawners. However, when the two spawning groups spawn at the same age, as they do in the Minch, there is some suggestion of a genetical control of growth-rate where a consistent difference in size is found. The greater age of the Atlanto-Scandian herring at first spawning, compared with the other three groups, also suggests a genetical difference.

Spawning time. While little is known in the herring there is good experimental evidence that spawning in teleosts is controlled by hormonal action (Hoar, 1951). Gonadectomy has been performed in fish, and results in the loss of secondary sexual characters. Mammalian androgens cause sexual precocity in males and masculinization of females.

The presence and action of gonadotropins have been demonstrated in fish by hypophysectomy and by the injection of gonadotropins. Hypophysectomy is followed by gonadial regression, while implantation of pituitary gland or injection of gonadotropic hormones results in accelerated sexual maturity.

Many workers have found a cycle in the ratio of acidophil to basiphil cells in the anterior lobe of the pituitary. In particular Buchmann (1940) reported this in *Clupea harengus*. Some factor however causes the pituitary to secrete hormones, and it seems likely that environmental conditions such as temperature or day length are responsible for this rather than an inherent rhythm. Baker and Baker (1936) have pointed out that it is unlikely that a biological system could incorporate an exact timing mechanism.

Temperature would seem to be an important factor, particularly in poikilotherms, though BULLOCK (1955) has shown that such animals have some independence of temperature changes. An artificial rise of temperature in experiments on some fish will induce early spawning. Artificial light conditions, usually adjusted to give the effect of seasonal changes in day length, but much accelerated, cause the early onset of maturity in some fish, while in others light conditions only accelerate maturity within an appropriate temperature range. There is also evidence that the pituitary is controlled by a nervous centre in the brain, and nervous pathways have been traced from the periphery to the hypothalmus and from there to the pituitary (reviewed by HOAR, 1951).

This work has been done mainly on small fish with well developed secondary sexual characters; very few data are available for commercially useful marine species. Indeed very few of these have secondary sexual characters and they are often difficult to breed in aquaria. This applies particularly to the herring, though OUTRAM (1951) reported that *Clupea pallasii* both matured and spawned in captivity. The lack of secondary sexual characters in marine fish of commercial value may be due to a more promiscuous spawning nature, where many fish congregate on a spawning ground. An account of the spawning act in *Clupea harengus* has been given by EWART (1883). Although the presence of other fish may be necessary to induce the spawning act, normal recognition of males and females may not be. Yet males and females may differ in behaviour, or in the production of some chemical stimuli, and recognition may be brought about in this way.

There are good grounds then for believing that, in the herring, maturation and spawning are controlled by hormones which are themselves environmentally controlled. These hormones may be responsible for the behaviour associated with the sexual cycle, including migration. Environmental influences which might control the timing of the spawning cycle of herring are food, temperature, salinity, light, social and topographical factors. A distinction must be made between stimuli affecting the maturation process and those triggering the spawning act.

(i) Food. At present, even in higher vertebrates, the extent to which feeding and maturity are related is not clear. SVÄRDSON (1951), however, found in coregonids that spermatogenesis and oogenesis were accelerated by lack of food.

Feeding in the herring is reduced during the winter as shown by HARDY (1924), SAVAGE (1937), and other workers. It is not known whether lack of food will prevent sexual development or only the development of a smaller number of eggs and spermatozoa, but it might be that increased feeding either before or after the winter could accelerate the maturation process. For all that, herring kept and fed for a year in this laboratory showed no signs of maturation at a time of year when they might have been expected to spawn in their natural habitat. Again, OUTRAM (1951) reported that maturation and spawning were later than normal in *Clupea pallasii* kept in aquaria. Feeding is likely to be inadequate in aquaria, but so are other conditions. In any event, while feeding may well be involved in maturation, it is not likely to be the stimulus triggering off the spawning act.

(ii) Temperature. There is some evidence in the field that both maturation and the spawning act may be dependent on temperature. RUNNSTRÖM (1941b) pointed out that Norwegian spring herring prefer certain temperature and salinity conditions for spawning. In particular JOHANSEN (1924) showed that spring spawning occurred at temperatures of 4°—7°C. and autumn spawning at 9°—14°C. SAHRHAGE (1954) showed that spring spawning occurs at temperatures between 6°—8°C. and autumn spawning between 12·5°—14°C.; his data however refer to 1953 only, which was a warm year, and it is doubtful whether such figures could be applied in other years. SAHRHAGE also found that the percentage of ripe fish on the Dieppe spawning grounds was very small in early December 1952 when the temperature was 2°C. below normal and that it was over 50% in early December 1953 when the temperature was 2°—3°C. above normal. DEVOLD (1955) suggested that cycles of abundance in the Norwegian and Swedish herring fisheries might be explained by temperature changes sufficient to alter the spawning time by three months.

If temperature were the factor controlling maturation, the more northerly North Sea autumn spawning fish would be reacting to rising temperature and those farther south, which spawn later, to rising, followed by falling, temperature. This implies there are two groups of fish with different triggering mechanisms. Perhaps the herring require an "accumulation" of temperature on the principle of "day-degrees" (TÅNING, 1944) in order to reach the fully mature state. If this is so of autumn spawners, possibly the northern spawners require a smaller accumulation than the southern spawners. This could account for early spawning in warm years and late spawning in cold years. On the other hand the fish may require a certain threshold temperature to trigger off spawning. In this case in a cold year the northerly autumm spawners might have to move farther south to find suitable conditions, and those in the south might be expected to spawn earlier if they respond to a threshold of falling temperature. It may well be that a combination of these factors occurs and that herring require a certain "accumulation" of temperature to bring on maturity while spawning is triggered off by a threshold temperature.

(iii) Salinity. It has been shown by various workers (see RUNNSTRÖM, 1941a, 1941b) that Norwegian spring herring spawn in water of salinity 32—34‰, that is, they avoid the more saline Atlantic water and less saline Baltic water. LE GALL (1935) showed that herring spawning grounds were limited by the inflow of Atlantic water. HOURSTON (1953) showed there was a tendency for shoals of *Clupea*

pallasii to be located in the slightly less saline water. Outram (1951) made the interesting observation that ripe specimens of *Clupea pallasii* were induced to spawn in aquaria, probably when fresh water was added. This evidence seems to indicate that salinity changes may be of some importance during spawning, and Le Danois (1949) has put forward the hypothesis that herring are in a sense anadromous fish, seeking less saline water to spawn. But it seems doubtful whether the maturation cycle of the herring could be controlled, or the spawning act triggered, by salinity changes alone though salinity might be a factor affecting the direction of migration (Craig, 1956).

(iv) Light. A light factor may be present in the behaviour, and therefore in the spawning act, of the herring. Savage and Hodgson (1934) have shown that catches at full moon periods are much higher in the East Anglian spawning herring fishery, and Hickling (1947) has shown that the phase of the moon may be of some importance in the fishery from Milford Haven. Jens (1954) found a tidal and lunar effect on German lugger catches in 1953.

The effect of day length on maturation in the herring has yet to be shown. It may well be that day length, either with or without a temperature factor, is involved in the initiation and control of the maturation cycle. Unlike temperature and salinity, day length would be a rigid stimulus, invariable from year to year, and giving a precise spawning season. If a temperature factor were involved this would not be so. If herring react to day length then spring and autumn spawners and the different groups of autumn spawners in the North Sea are genetically distinct.

(v) Others. Factors which may be also important in triggering the spawning act are those of contact with the opposite sex and the availability of a suitable ground for spawning. Thus it seems that the maturation cycle may be controlled by temperature, day length, and food supply, while the spawning act is triggered by a combination of factors which may include temperature, behaviour, and topography, as well as possible chemical ones as yet undiscovered.

How then do these facts throw light on the genetical or other distinction between spring and autumn spawners? If it is agreed that herring spawning is most likely mediated by hormonal factors, ultimately dependent on changes in environmental conditions, it must be shown how spawning could occur at different times. Spawning at different times of year implies that herring of the two groups are responding to different environmental stimuli or to different values of the same stimulus. In some areas (Minch, Firth of Forth, Moray Firth), mixed shoals of spring and autumn spawners live together during adolescence. They are therefore both subject to the same conditions during the year. If spawning were wholly dependent on external conditions, then one would expect the two groups to spawn contemporaneously, unless they differ genetically. If the reaction of the two groups differs with respect to the same environment, it can only be due to difference in genotype.

It could even be argued that spawning is entirely independent of the environment. Thus, for instance, a spring spawned herring might be due to spawn a certain number of complete years after birth, and an autumn one, though of similar genotype, the same. This would automatically cause segregation into two spawning groups, but it is difficult to see how such circumstances first arose. If the spawning is to be a certain number of years after birth, such a period surely must be timed by external conditions.

It may, however, be concluded from the foregoing that the nature of the differences in the two spawning groups is likely to be at least in part genetical. This seems most probable for the spawning processes themselves and less likely for the other group characteristics. It is perhaps unfortunate that the meristic characters on which the herring races are largely based, are most in doubt in this respect—particularly in so far as these are used to differentiate other than the seasonal spawning groups. This emphasizes that future herring "racial" work should take into consideration as many differences as possible, but perhaps concentrate on the spawning processes relative to the environment.

III. The Status of the Herring Groups

If there are reasons to believe that herring "races" may be genetic it is necessary to allot the groups to taxonomic categories.

Mayr (1942) gives a shortened definition of the species sufficient for this paper: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups". A sub-species is defined as "a geographically localized subdivision of a species which differs genetically and taxonomically from other subdivisions of the species". This geographical localization need only occur during the breeding season and interbreeding may take place where the ranges of the different sub-species meet.

In order to evaluate these terms it is necessary to think of the process of speciation in a dynamic sense. Divergence first occurs when the distribution and frequency of genes comes to differ in different populations. If this differentiation is not checked by interbreeding, further isolating mechanisms may be set up which prevent the possibility of crossing and at this stage races become species, as they are reproductively isolated. Races or sub-species represent stages in an evolutionary trend which may develop further; they are potentially incipient species.

In typical spring and autumn spawning herring groups reproductive isolation obviously exists although interbreeding is not perhaps impossible across the

extremes of seasonal range. Prima facie then spring and autumn spawning herring might be referred to different species. The principal objection to such a thesis lies in the morphological similarity of the two groups. This may be overcome by calling them "sibling species", defined as different but co-existent species which are very similar morphologically.

THORPE (1940) pointed out that some sibling species are so alike that they can only be distinguished on biological grounds. Usually they may be separated by slight morphological characters or a difference in ecology such as food or habitat. Co-existent species with the same ecology are unlikely to exist for long (GAUSE, 1934).

LISSNER (1934) considered that spring and autumn spawners are sub-species, divided into different races and divided again into local forms: neither races nor local forms being genotypic units. KREFFT (1955) has rightly pointed out that sub-species and races should be equated. KREFFT also referred spring and autumn spawners to different sub-species although he considered that difference in spawning time is inadequate for the formation of sub-species ("Subspeziesbildung").

It should be emphasized that a sub-species may only be geographically separate from other species during the spawning time and co-existence at other times need not invalidate the status of sub-species. The two main groups of herring considered here are, however, typically localized geographically (they nearly always use different spawning grounds) and isolated temporally, during the spawning season. Temporal isolation is something more than the geographical localization usually found in sub-species where there is often interbreeding in those places where sub-species meet. Geographical localization would seem to be a less drastic barrier to interbreeding than temporal isolation, particularly in the sea. The question of whether such categories as temporal sub-species can be postulated, or whether these should be referred to as species, has been neglected by systematists. If the current definition of a species (which uses as its main tenet the question of reproductive isolation) is to hold then it would seem that absolute difference in breeding season should be an adequate criterion for assigning specific status.

Again one must consider the dynamic aspect of this problem. As SIMPSON (1951) has pointed out the final verdict should depend on a prediction of what will happen in the future. If the herring groups are likely to continue along divergent or parallel paths, with insufficient gene flow between them to cause a convergence, then they should be considered as good species. With this in mind, it is suggested that the spring and autumn spawning herring considered in this report may be referred to different sibling species. The similarity between them might be due to either a recent divergence, or possibly to lack of competition between them sufficient to cause either further divergence or elimination of one group. A comparative study of the ecology of the two groups might yield valuable information.

How then do these conclusions fit the two main comparisons which are to be made? The Atlanto-Scandian and Minch spring spawning herring may be considered as sub-species of one species. There seems no question that interbreeding would take place if they were found together during the spawning season. The Minch and North Sea autumn spawners may be considered as another species.

IV. Reproductive Isolation in the Herring

The amalgamation of two genetically distinct groups is possible by interbreeding. Where this occurs any limiting characters may take an intermediate and often highly variable form in the hybrids. Where the groups are good species, hybrid crosses may be inviable, or, if progeny are produced, they may not be fertile. For all that, fertile interspecific fish hybrids have been produced.

In the herring, the typical spring and autumn spawners are ecologically isolated and could interbreed only by change of spawning season. BLAXTER (1956a) hatched spring and autumn spawned herring eggs at different temperatures and found that there was no significant difference in percentage hatching of autumn spawned larvae at temperatures between 5·5°C. and 14·5°C. but that in spring spawned larvae the percentage hatching was significantly lower at the high temperatures than at the lower ones. Under experimental conditions then the spring spawned eggs were markedly inviable at autumn spawning temperatures. BLAXTER (1955) has also found that spring spawners from the Scottish west coast can be crossed with autumn spawners from the east coast. The fact that the groups can be crossed in no way invalidates the conclusion that the groups are good species, as natural reproductive isolation has been broken down by artificial means. Providing this does not or cannot happen under natural conditions, or if it does, that the hybrids are sterile, or markedly inviable, there is no reason to use such a criterion as an argument for amalgamating species. But what must finally determine different species is the extent of gene flow between them. Provided this is inadequate to cause convergence the species remain separate.

In the herring evidence has come to light recently which may indicate some interchange between spring and autumn spawners. Work has shown that spring and autumn spawners have characteristic otoliths (EINARSSON, 1951; PARRISH, 1954). BAXTER and PARRISH (personal communication) report that very occasionally a fish ripe in spring may be found with a characteristically autumn type of otolith. These facts, together with the considerable seasonal spread

of the "autumn" spawning season, suggest there might be a small interchange, but whether this occurs between one spawning season and the next, or whether the young of a particular group change at their first spawning season, is not clear. In the former case a herring might spawn either twice in a year or leave a gap of eighteen months between spawning. If such an interchange occurs it can only affect the specific status of the two groups if it causes them to converge.

Wright's (1931) population studies include an analysis of the effect of spatial migration on genetical divergence and evolution, and there seems no good reason why his results should not be applied to migration in time. He concludes that only a very small interchange may be required to prevent divergence. In an idealized case he states that the exchange of one breeding individual every other generation might prevent divergence regardless of the size of the colony. On the other hand an interchange of the order of thousands of individuals per generation in neighbouring subgroups of a widely distributed species might be insufficient to prevent a random drift apart. Though it is impossible to apply such conclusions to the herring, it may be said that the number of possible changeover fish which have been detected is very small. Considering the extent of sampling though, it might represent thousands of changeover fish in the herring stocks.

The changeover, if it exists, might well be above the critical value, and so the result should be a progressive convergence of the stocks (with possibly an intermediate breeding season). This is certainly not obviously occurring though it might be slow, and a difficult process, to detect. The work of Rasmussen (1939) and Runnström (1941 b), who showed a progressive delay in the spawning of Norwegian herring, could be explained by saying that interbreeding with autumn spawners was giving a late spawning season, but it is perhaps more likely to be due to change in environmental circumstances. It is also true that the spring spawners in the north-west North Sea have much decreased of late. Could this be due to interbreeding with autumn spawners? An intermediate spawning season might have poor survival value and not be perpetuated due to lack of food for the larvae. It seems more likely that convergence is not occurring. In this case the alternatives are either that interchange does not take place, or if it does, it is insufficient to cause convergence of the groups. It does not seem likely that interchange would be sufficient to prevent morphological divergence and yet be inadequate to cause convergence of other characteristics such as spawning.

V. Origin of the Herring Groups

Allopatric speciation (i. e., speciation by progressive divergence of sub-species or geographically replacing forms of a species) is generally held as the most common, if not the only method of speciation in animals (Mayr, 1942, 1947; Lack, 1944, 1947; Rensch, 1947; Svärdson, 1949). If this is accepted we may speculate on the ways in which the different herring groups were formed.

Let us suppose, for example, that the ancestral herring stock spawned once per year, in the spring, temperature being the main factor controlling spawning. The stock was next isolated into two or more groups by the development of a land barrier or perhaps by the southward movement of ice from the Arctic. One group might have found itself in an area of higher temperature than previously experienced. If the temperature in the new environment never dropped to the values normally encountered for spring spawning, the group might have to adapt itself to a higher spawning temperature, perhaps by the survival of the offspring of those fish which had previously spawned at somewhat higher temperatures than the main body.

When isolation was broken down by the restoration of the original conditions, this group of high temperature spawners would not be able to interbreed with those groups which had been able to maintain a low temperature or spring spawning season.

Such speculations might be applied in a different way if the ancestral stock were autumn spawning or if it spawned twice per year.

VI. Conclusions

It is suggested that the Atlanto-Scandian and Minch spring spawning herring may be considered as sub-species of one sibling species, and that the North Sea and Minch autumn spawners may be considered as another sibling species. This conclusion is reached using the main criterion of difference in breeding season.

Morphological and meristic character differences between the species and sub-species seem to be controlled mainly by the environment at the spawning season, but evidence has been put forward that the difference in spawning season is genetical and is based on different responses to the environment.

A more satisfactory nomenclature for spring and autumn spawners might be low and high temperature spawners. The high temperature spawners would then include all those herring spawning in the North Sea from August to December and those herring in the Minch, Irish Sea, and elsewhere which spawn in the

autumn. The low temperature spawners would include those fish mainly of Atlantic origin which spawn in February and March.

It is suggested that the two main spawning groups arose by allopatric speciation from a single parent stock. Their morphological similarity is attributed to either the comparatively recent evolution of the groups, or to insufficient competition between them to cause divergence.

The conclusions reached need not invalidate the characters used in sampling work provided their fallibility is realized. Where possible a combination of characters is more satisfactory than one alone.

Svärdson (1948—1953) in his work on the coregonids of Sweden comes to very similar general conclusions with groups of fish that also differ in meristic characters, size, and spawning season. In some cases the meristic characters and growth-rate have been modified by changing environmental conditions in various ways. Some characters appear to be partly inherited with intermediate but probably partially sterile hybrids.

VII. A Possible Programme for Further Work

1. Experiments to determine the physiology of spawning in herring,
   (a) by keeping herring in aquaria under different conditions;
   (b) by endocrinology studies (i. e., hypophysectomy, gonadectomy, injection of hormones), including histological changes in the endocrine glands of herring.
2. Experiments to discover whether herring change over their spawning seasons,
   (a) by tagging of ripe fish;
   (b) by examining racial characters.
3. Experiments to determine the nature of differences in the groups,
   (a) by rearing herring under different conditions to observe differences in anatomical, meristic, and physiological characters;
   (b) by further work on crossing the groups;
   (c) by looking for biochemical differences (by electrophoresis, immunology, etc.);
   (d) by further work on anatomical differences.

Acknowledgements

I am most grateful for the advice of Dr. A. J. Cain of the Department of Zoology and Comparative Anatomy, Oxford.

Professor A. C. Hardy, Linacre Professor of Zoology at Oxford, and my colleagues Dr. H. Wood, Mr. B. B. Parrish, Mr. R. E. Craig, and Mr. I. G. Baxter read this paper in manuscript and made many helpful suggestions.

References

Andersson, K. A., 1947. "The stock of herring in the Sound and the southern Baltic in the years 1940—1944." Ann. Biol., Copenhague, **2**: 166.

Anon., 1938. "Morphological characteristics of the population of the Barents Sea herring (*Clupea harengus* L.)." Trans. Knipovich Polyar. Sci. Inst., **1**: 59.

Baker, J. R., & Baker, I., 1936. "The seasons in a tropical rain forest (New Hebrides). Pt. 2. Botany." J. Linn. Soc. (Zool.), **39**: 507.

Baxter, I. G., see
Wood, H., *et al.* 1952. — Ann. Biol., Copenhague, **8**: 147.
Parrish, B. B., *et al.* 1953. — Ann. Biol., Copenhague, **9**: 185.
Parrish, B. B., *et al.* 1954. — Ann. Biol., Copenhague, **10**: 163.
Parrish, B. B., *et al.* 1956. — Ann. Biol., Copenhague, **11**: 134.

Baxter, I. G., 1953—56. Unpubl. data.

Blaxter, J. H. S., 1955. "Herring rearing — I. The storage of herring gametes." Mar. Res. Scot., 3.

— 1956. "Herring rearing — II. The effect of temperature and other factors on development." Mar. Res. Scot., 5.

— 1957a. "Herring rearing — III. The effect of temperature and other factors on myotome counts." Mar. Res. Scot., 1.

Blaxter, J. H. S., 1957b. "The cranial osteology of the herring in racial investigations." This volume, p. 20.

Buchmann, H., 1940. "Hypophyse und Thyroidea im Individualzyklus des Herings." Zool. Jb. Anat., **66**: 191.

Bückmann, A. 1950. "Die Untersuchungen der Biologischen Anstalt über die Ökologie der Heringsbrut in der südlichen Nordsee." Helgoländ. Wiss. Meeresunters., **3**: 171.

Bullock, T. H., 1955. "Compensation for temperature in the metabolism and activity of poikilotherms." Biol. Rev., **30**: 311.

Cox, P., 1923. "Regional variation in the four-spined stickleback *Apeltes quadracus* Mitchell." Canad. Field Nat., **37**: 146.

Craig, R. E., 1956. Unpubl. data.

Cushing, D. H., 1955. "On the autumn-spawned herring races in the North Sea." J. Cons. Int. Explor. Mer, **21** (1): 44.

Davis, F. M., 1936. "A contribution to the race question." Rapp. et Proc.-Verb., **100**: 12.

Dannevig, A., 1932. "Is the number of vertebrae in cod influenced by light or high temperature during the early stages?" J. Cons. Int. Explor. Mer, **7** (1): 60.

— 1948. "Rearing experiments of Flødevigen sea fish hatchery." J. Cons. Int. Explor. Mer, **15** (3): 277.

— 1950. "The influence of temperature on number of vertebrae in plaice." Fiskeridir. Skr. Havunders., **9** (9): 1.

Devold, F., 1955. "Scandinavian herring periods." ICES, Herring Committee, Paper 69.
Ege, V., 1942. "A transplantation experiment with *Zoarces viviparus* L." C.R. Lab. Carlsberg (Ser. Physiol.), **23**: 17.
Einarsson, H., 1951. "Racial analysis of Icelandic herring by means of the otoliths." Rapp. et Proc.-Verb., **128** (1): 55.
Ewart, J. C., 1883. "The natural history of the herring." Rep. Fish. Bd. Scot., **2**: 61.
Farran, G. P., 1938. "On the size and number of the ova of Irish herring." J. Cons. Int. Explor. Mer, **13** (1): 91.
Friðriksson, Á., & Timmermann, G., 1951. "Some remarks on the eggs of herring . . . etc." J. Cons. Int. Explor. Mer, **17** (3): 261.
Gabriel, M. L., 1944. "Factors affecting the number and form of vertebrae in *Fundulus heteroclitus*." J. Exp. Zool., **95**: 105.
Gause, G. F., 1934. *The Struggle for Existence.* Baltimore: Williams and Wilkins.
Hardy, A. C., 1924. "The herring in relation to its animate environment. Pt. I. The food and feeding habits of the herring." Fish. Invest. Lond., **7** (3): 1.
Heincke, F., 1898. "Naturgeschichte des Herings." Abh. Dtsch. Seefisch Ver., **2**.
Hempel, G., 1953. "Die Temperaturabhängigkeit der Myomerenzahl beim Hering (*Clupea harengus* L.)." Naturwissenschaften, **17**: 467.
Heuts, M. J., 1949. "Racial divergence in fin ray variation patterns in *Gasterosteus aculeatus*." J. Genet., **49**: 183.
Hickling, C. F., 1947. "The herring fisheries at Milford Haven." J. Mar. Biol. Ass. U.K., **26** (3): 408.
Hjort, J., 1909. "Report regarding the herring." Rapp. et Proc.-Verb., **12** (5): 3.
Hoar, W. S., 1951. "Some aspects of the physiology of fish. Hormones in fish." Univ. Toronto Stud. Biol., 59.
Hodgson, W. C., 1934. *The Natural History of the Herring of the Southern North Sea.* London: Arnold. (Buckland Lecture).
— 1950. Ann. Biol., Copenhague, **6**: 175.
Hourston, A. S., 1953. "The relationship of herring in inshore water to the temperature and salinity of the environment." Progr. Rep. Biol. Stat. Nanaimo, 96: 15.
Hubbs, C. L., 1925. "Racial and seasonal variation in the Pacific herring . . ." Calif. Fish Game, **8**: 1.
Huntsman, A. G., 1919. "Variation of fishes according to latitude." Science, **50**: 592.
Huxley, J. S., 1932. *Problems of Relative Growth.* London: Methuen.
Jens, G., 1954. "Untersuchungen über rhythmische Erscheinungen beim Heringsfang in der Nordsee." Arch. Fischereiwiss., **5**: 113.
Johansen, A. C., 1919. "On the large spring-spawning sea herring (*Clupea harengus* L.) in the north-west European waters." Medd. Komm. Havunders., **5** (8): 1.
— 1924. "On the summer and autumn spawning herring of the North Sea." Ibid., **7** (5): 1.
Krefft, G., 1954. "Untersuchungen zur Rassenfrage beim Hering." Mitt. Inst. Seefisch., **6**: 12.
Krefft, G., Schubert, K., & Sahrhage, D., 1955. "Der augenblickliche Stand der Erforschung des Nordseeherings . . ." Arch. Fischereiwiss., **6**: 141.
Lack, D., 1941. "Ecological aspects of species formation in passerine birds." Ibid, **86**: 260.
— 1947. *Darwin's Finches.* Cambridge: University Press.
Le Danois, E., 1949. *Vie et Mœurs des Poissons.* Paris: Payot.
Lea, E., 1929. "The oceanic stage in the life history of the Norwegian herring." J. Cons. Int. Explor. Mer, **4** (1): 3.
Le Gall, J., 1935. "Le hareng *Clupea harengus* Linné. 1. Les populations de l'Atlantique Nord-Est." Ann. Inst. Océanogr., **15** (1).
Lissner, H., 1934. "On the races of herring." J. Cons. Int. Explor. Mer, **9** (3): 346.
Martin, W. R., 1949. "The mechanics of environmental control of bodyform in fishes." Publ. Ontario Fish. Res. Lab., 58.
Mayr, E., 1942. *Systematics and the Origin of Species.* New York: Columbia University Press.
— 1947. "Ecological factors in speciation." Evolution, **1**: 263.
McHugh, J. L., 1942. "Vertebral number of young herring in southern British Columbia." J. Fish. Res. Bd. Can., **5**: 474.
Meyer, H. A., 1878. "Beobachtungen über das Wachsthum des Herings im westlichen Teile der Ostsee." Wiss. Meeresuntersuch., **3**: 227.
Mottley, C. McC., 1937. "The number of vertebrae in the trout." J. Biol. Bd. Can., **3**: 169.
Outram, D. N., 1951. "Observations on the retention and spawning of the Pacific herring." Progr. Rep. Biol. Stat. Nanaimo, 87: 32.
Parrish, B. B., 1954. Advan. Sci. (synopsis of talk in programme for 1954 meeting).
Rasmussen, T., 1939. "Fluktuasjoner i vintersildens utvikling og gytning." (English Summary). Rep. Norweg. Fish. Invest., **6**: 70.
Rensch, B., 1947. *Neuere Probleme der Abstammungslehre.* Stuttgart: Enke.
Rounsefell, G. A., 1930. "Contribution to the biology of the Pacific herring *Clupea pallasii* and the condition of the fishery in Alaska." Bull. U.S. Bur. Fish., **45**: 227.
Rounsefell, G. A., & Dahlgren, E. H., 1932. "Fluctuations in the supply of herring *Clupea pallasii* in Prince William Sound Alaska." Bull. U.S. Bur. Fish., **47**: 263.
Runnström, S., 1933. "Über die Rassenverhältnisse bei dem norwegischen Frühjahrshering . . ." J. Cons. Int. Explor. Mer, **8** (2): 235.
— 1936. "A study on the life history and migrations of the Norwegian spring herring . . ." Fiskeridir. Skr. Havunders., **5** (2): 1.
— 1941a. "Racial analysis of the herring in Norwegian waters." Ibid., **6** (7): 1.
— 1941b. "Quantitative investigations on herring spawning and its yearly fluctuations at the west coast of Norway." Ibid., **6** (8): 1.
Sahrhage, D., 1954. "Beobachtungen zur Frage der Heringslaichplätze." Mitt. Inst. Seefisch., **6**: 24.
Savage, R. E., 1937. "The food of the North Sea herrings." Fish. Invest. Lond., **15** (5): 1.
Savage, R. E., & Hodgson, W. C., 1934. "Lunar influence on the E. Anglian herring fishery." J. Cons. Int. Explor. Mer, **9** (2): 223.
Schach, H., 1939. "Die künstliche Aufzucht von *Clupea harengus* L." Helgoländ. Wiss. Meeresunters., **3**: 359.
Schmidt, J., 1917. "Racial Investigation II." C.R. Lab. Carlsberg, **14** (1): 11.
— 1919. "Racial Investigation III." Ibid., **14** (5): 1.
— 1920. "Racial Investigation V." Ibid., **14** (9): 1.
— 1921. "Racial Investigation VII." Ibid., **14** (15): 19.
Schultz, L. P., 1927. "Temperature controlled variation in the golden shiner *Notemigonus crysoleucas*." Pap. Mich. Acad. Sci., **7**: 417.
Schnakenbeck, W., 1929. "Entwicklungsgeschichtliche und morphologische Untersuchungen am Hering." Ber. Dtsch. Komm. Meeresforsch., **5**: 19.
— 1931. "Zum Rassenproblem bei den Fischen." J. Cons. Int. Explor. Mer, **6** (1): 28.
Simpson, G. G., 1951. "The species concept." Evolution, **5**: 285.

Svärdson, G., 1949. "The coregonid problem I . . ." Rep. Inst. Freshw. Res. Drottningh., 29: 89.
— 1950. "The coregonid problem II . . ." Ibid., 31: 151.
— 1951. "The coregonid problem III . . ." Ibid., 32: 79.
— 1952. "The coregonid problem IV . . ." Ibid., 33: 204.
— 1953. "The coregonid problem V . . ." Ibid., 34: 141.
Tåning, Å. V., 1944. "Experiments on meristic and other characters in fishes." Medd. Komm. Havunders., Kbh., **11** (3): 1.
— 1952. "Experimental study of meristic characters in fishes." Biol. Rev., **27**: 169.
Tester, A. L., 1937. "Population of herring (*Clupea pallasii*) in the coastal waters of British Columbia." J. Fish. Res. Bd. Can., **3**: 108.
Tester, A. L., 1938. "Variation in the mean vertebral count of herring (*Clupea pallasii*) with water temperature." J. Cons. Int. Explor. Mer, **13** (1): 71.
Thorpe, W. H., 1940. "Ecology and the future of systematics." In *The New Systematics* ed. by J. Huxley. Oxford: University Press.
Wood, H., 1932. "The natural history of the herring in Scottish waters." Aberdeen: Fishing News. (Buckland Lecture).
— 1936. "Race investigation of the herring population of Scottish waters." Sci. Invest. Fish. Scot., 1936, 3.
Wright, S., 1931. "Evolution in Mendelian populations." Genetics, **16**: 97.

2.

The Cranial Osteology of the Herring in Racial Investigations

By J. H. S. Blaxter,
Marine Laboratory, Aberdeen

Introduction

The skull of the herring (*Clupea harengus* L.) has been described by Matthews (1886) and Ridewood (1904). Apart from one Russian publication (Anon., 1938) there appears to be no work comparing the morphological characters of dermal bones of herring of different "racial" type. Ford (1948), however, found variations in the dermal bones of cod from different areas.

If differences existed they might supply another means of designating the origin of individual herring without making measurements or counts of other characters on samples of herring. Study was therefore made of the cranial osteology of herring from different areas with the primary object of looking for differences which might show whether individual herring were spring or autumn spawners.

Methods

Dermal and other bones of herring were prepared by boiling and cleaning and then examined under a binocular microscope. Observations were also made of bones *in situ*. The following were studied:— dentary, articular, maxilla, suboperculum, preoperculum, operculum, hyomandibular, ceratohyal, epihyal, clavicle, and cleithrum. Differences were looked for in shape, in the processes and foramina, in colour and translucency and in the position of the bone relative to other bones and parts of the head.

The main characters used in determining the type of herring were vertebral number, otolith type, and maturity stage.

Results

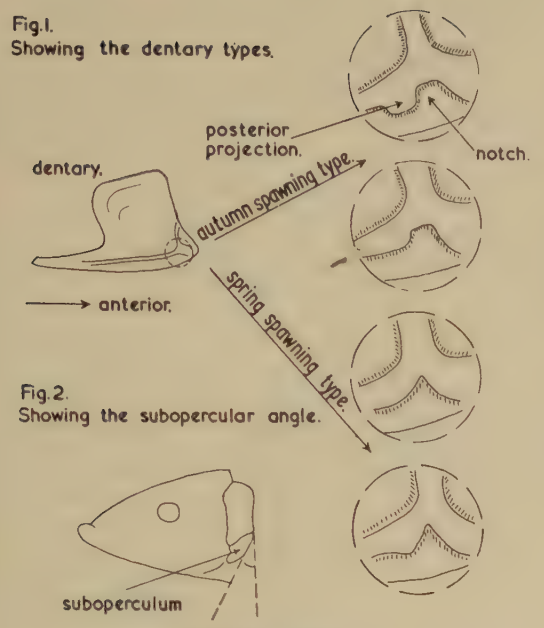
1. No consistent differences were observed in any bone except the dentary.

2. On examination of the dentary differences in the anterior angle of the bone were found in herring of different spawning type. These differences, which occurred in that part of the bone surrounding the lateral line system of the dentary, are shown in Figure 1. They are typical although detailed variation is found. In general the chief diagnostic characters are the postero-dorsal border of the notch which in the spring type is straight or slightly curved and in the autumn type with a distinct angle, and the antero-dorsal angle which in the spring type is usually about 45° and less than 90° and in the autumn type about 90° or more than 90°. A posterior projection is usually found in the autumn type but less commonly in the spring type.

3. After this difference had been detected, samples from various fisheries were examined and 883 pairs of dentaries allocated to the spring or autumn category. The results, checked by mean vertebral counts, are shown in Table 1.

Table 1

Position of sample and date	Mean vertebral counts of fish designated into groups by dentary: Autumn spawning	Spring spawning	Not known
Shetland 18/6/54	56·59 (27)	57·00 (1)	—
– 19/6/54	56·63 (8)	57·00 (18)	—
– 17/5/55	56·45 (40)	56·80 (5)	57·00 (3)
– 18/5/55	56·52 (25)	56·95 (21)	56·50 (2)
– 19/5/55	56·64 (33)	56·73 (11)	—
– 21/5/55	56·69 (26)	57·06 (18)	56·00 (3)
– 18/8/55	56·37 (43)	56·80 (5)	56·00 (2)
– 19/8/55	56·59 (44)	57·25 (4)	—
Clyde 3/3/55	57·00 (9)	57·03 (60)	56·90(21)
S. Minch 23/9/54	56·49 (41)	57·00 (11)	56·00 (3)
N. Minch 31/3/55	57·00 (6)	56·93 (40)	57·00 (1)
Coral Bank 23/3/55	56·48 (29)	56·83 (18)	— —
– 11/4/55	— —	57·04 (45)	— —
– 13/4/55	56·37 (27)	56·53 (15)	56·43 (7)
Fladen 23/8/54	56·31 (16)	56·60 (10)	— —
– 23/8/54	56·46 (41)	57·00 (3)	56·50 (2)
Gut 1/9/54	56·75 (28)	56·00 (1)	57·00 (1)
Scot. East Coast 15/7/54	56·31 (16)	56·75 (4)	— —
– 2/9/54	56·68 (16)	57·00 (3)	— —
– 9/9/54	56·44 (45)	56·50 (4)	57·00 (1)
	56·53(520)	56·93(297)	56·65(46)



Figures 1 and 2.

It will be seen that the division by dentary gives vertebral counts consistent with one group being composed mainly of autumn spawners and the other mainly spring spawners. The division is not, however, complete. It is estimated from the above table and using maturity stage and otolith type that the dentary can be used to allot a fish to its correct spawning group in nine cases out of ten. Generally the Shetland and Scottish east coast fish were easily divided into spawning groups. The most difficult sample to reconcile to the main dentary types was a sample of spawning fish caught in the Clyde in March 1955, of which 60 were appropriately designated as spring spawners. Nine others had a definite autumn spawning type of dentary inconsistent with maturity, otolith type and vertebral count, while twenty-one fish had either a different type of dentary on each side of the head or else abnormal dentaries with occluded notches.

The dentaries of 46 Norwegian herring of unknown vertebral count were also examined. In general the dentary characters were rather coarser and more difficult to separate than those of the other fish examined (probably due to the fact that they were larger fish). Thirty-one fish had dentaries of the spring type, four of the autumn type, and nine fish had dentaries which could not be designated. The otoliths of this sample indicated that they were all spring spawning fish. One fish with this coarse type of dentary, found in a Shetland sample, had an otolith of characteristically Norwegian type.

Table 2

Position of sample and date	Mean angle left hand side (numbers of fish)		Mean angle right hand side (numbers of fish)		Difference
Peterhead 2/6/54	17·7°	(49)	26·8°	(43)	9·1°
Lerwick 4/6/54	16·4°	(45)	21·3°	(45)	4·9°
Lerwick 5/6/54	20·0°	(43)	25·9°	(47)	5·9°
S. Minch 10/6/54	13·5°	(49)	20·1°	(48)	6·6°
Lerwick 11/6/54	14·5°	(46)	22·5°	(48)	8·0°
Lerwick 12/6/54	12·9°	(44)	19·7°	(46)	6·8°

This method of race determination is not as certain as the otolith method but it can be used on a sample of fish without treatment of the bones by placing the snout under a binocular microscope and teasing away the tissues overlying the anterior part of the dentary. It could therefore be of value in estimating the proportion of spring and autumn spawners in a sample, or for picking out one group from the other if work was only required on a particular spawning group. It is possible that dentary characters may be of value in other herring groups, such as those of the Baltic.

An important negative result of this work is that no completely certain, easily identifiable, osteological character has been found by which individual spring and autumn spawners can be separated. The dentary will probably give a correct answer in 90% of cases.

4. Another bone, the suboperculum, also proved to be of interest. Observations of this bone *in situ* showed that the angle between its posterior border and the vertical was different on either side of the head. On the right hand side the angle to the vertical was greater. The herring skull is thus slightly asymmetrical.

Figure 2 shows the angle measured and in Table 2 the differences in the angles are shown.

Acknowledgements

I should like to acknowledge with thanks the help and advice of my colleagues, Mr. B. B. Parrish and Mr. I. G. Baxter.

References

Anon., 1938. "Morphological characteristics of the population of the Barents Sea herring (*Clupea harengus* L.)." Trans. Knipovich. Polyar. Sci. Inst., **1**: 59.

Ford, E., 1948. "The neurocranium of the cod." Abstract of paper given before Challenger Society at Plymouth 9/10 July 1947.

Matthews, J. D., 1887. "On the structure of the herring and other clupeoids. Part I. The skeleton." Rep. Fish. Bd. Scot., **5**: 257.

Ridewood, W. G., 1904. "On the cranial osteology of clupeoid fishes." Proc. Zool. Soc. Lond., **2**: 448.

3.

Counting of Gill Rakers as a Method of Morphological Herring Investigations

By Gerhard Krefft
Institut für Seefischerei, Hamburg

Since the work of Heincke (1898) the number of vertebrae (VS) and of the keeled scales (K_2), and partly the number of precaudal vertebrae have been used for the characterization of different biological groups of herrings (*Clupea harengus* Linnaeus). The counts of precaudal and caudal vertebrae, and to some degree the counts of K_2 are liable to certain sources of error. Therefore many workers restricted themselves to VS counts. In search of other meristic characters of similar variation but less liable to error I began to count the number of gill rakers of the first left arch. This method is commonly used for taxonomical purposes, especially to discriminate between closely related forms, e. g., in *Alosa* and *Sardinella* species. The first results of these gill-raker counts in herrings were published in my paper of 1954. Since then I have investigated a rather comprehensive material. The numbers of vertebrae and keeled scales were also recorded.

Technical observations

Gill rakers are best counted when dry. Only the rakers of the lower branch of the first arch are counted, i. e., those of the ceratobranchial and the hypobranchial. There is little variation in the number of rakers in the epibranchials; it is moreover difficult to find the boundary between the first two epibranchials.

The gill arch is removed by means of scissors. The tongue should remain attached to the arch in order to retain the foremost gill rakers. These are often bud-shaped. The gill arches are then pinned on boards furnished with nails and are allowed to dry. The rakers may be counted immediately after drying or be kept in paper-bags marked with serial numbers for subsequent investigation. The counts are made by means of a binocular lens (magnification $\times 10$). There is no difficulty in discerning the last rakers of the upper and lower branch. If, however, the foremost raker is bud-shaped, it is sometimes difficult to perceive and may easily be passed over by inexperienced operators.

The relation between body length and number of gill rakers

While the numbers of vertebrae and keeled scales are individually constant after metamorphosis, there may be an increase of the number of gill rakers with the increasing body length. There is a positive correlation between the two variates, of some importance in young herring only, but very insignificant in mature fish.

In a sample of 1030 late winter spawners of the Atlantic type (only mature specimens stage IV—VI, 25—39 cm. in length) I found a correlation coefficient $r = + 0{\cdot}182 \pm 0{\cdot}03$. In 1065 mature Bank herrings from Bressay Shoal to southern Long Forties r was only $+ 0{\cdot}091 \pm 0{\cdot}003$. In Figure 1 the relation between length and average number of gill rakers of the two samples is represented graphically. The average values were smoothed according to the formula

$$f_i = \frac{f_{(i-1)} + 2 f_i + f_{(i+1)}}{4}$$

Immature herring, however, show a lower number of gill rakers distinctly increasing with length. In racial investigations it is therefore important to consider the length of the fish.

The number of gill rakers as a racial character

When comparing the diagrams (Fig. 1) of the average number of gill rakers of Atlantic and North Sea Bank herring of equal lengths it is easily seen that there is a difference of about two rakers. This

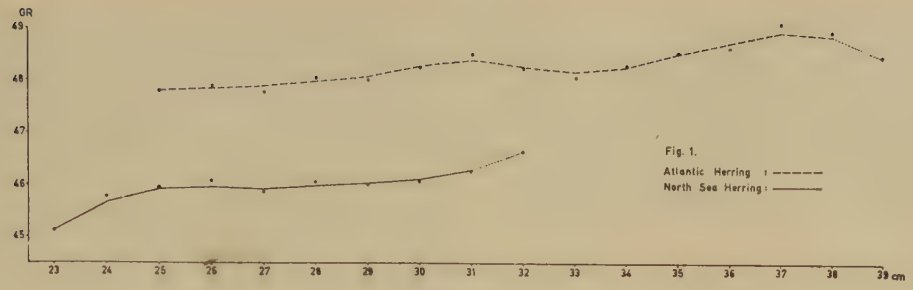


Figure 1.

difference is much more pronounced than that of the average number of vertebrae or the number of keeled scales.

Figure 2 shows the percentage distribution of gill-raker numbers of herring of comparable lengths from the same two sets of samples.

The figures are set out in Table 1.

The intergradation was calculated according to GINSBURG, 1938.

This is the area of overlapping of the two histograms, expressed as percentage of the total area of both. The intergradation was $\frac{45{\cdot}83}{2} = 22{\cdot}9$. This is a divergence of $100 - 22{\cdot}9 = 77{\cdot}1$ between the two herring populations. According to GINSBURG populations which in their character of greatest divergence differ by 75—85% are to be considered as subspecies on the presumption that the characters involved are genetically fixed. The average number of gill rakers in the autumn spawners is $46{\cdot}017 \pm 0{\cdot}045$, in the late winter spawners it is $48{\cdot}169 \pm 0{\cdot}059$, the difference being $2{\cdot}152 \pm 0{\cdot}074$, which is highly significant.

In a sample containing a mixture of both herring groups, the adults can easily be separated according to maturity. Difficulties may arise in the case of individuals of maturity stage II which may be either autumn spawners which ripen late in the year, or late winter spawners, or even immature fish of both groups. Individual discrimination is impossible on the basis of the counts of vertebrae and keeled scales only. When we add the gill-raker counts, however, it may be possible to draw a certain distinction between the two groups.

The analysis of a sample of herring from Bressay Shoal ("Anton Dohrn", Stat. 320, 14. August 1955) may serve as an example.

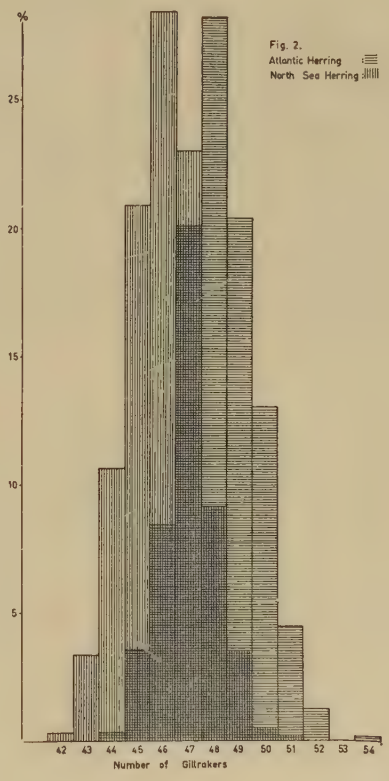


Figure 2.

Table 1

	Gill rakers													
	42	43	44	45	46	47	48	49	50	51	52	53	54	Total
Autumn spawners ...	3	33	104	206	280	227	90	35	5	2	—	—	—	985
%	0·30	3·35	10·65	20·91	28·43	23·04	9·14	3·55	0·51	0·22	—	—	—	100
Late winter spawners	—	—	2	23	55	131	184	133	85	29	8	—	1	651
%	—	—	0·31	3·53	8·45	20·12	28·26	20·43	13·06	4·46	1·23	—	0·15	100
			0·31	3·53	8·45	20·12	9·14	3·55	0·51	0·22				45·83

Number of gill rakers

Maturity ...	42	43	44	45	46	47	48	49	50	n
I—II	1	1	2	3	4	6	10	4	1	32
	$M_1 = 46{\cdot}875 \pm 0{\cdot}319$									
III—VI..	1	3	5	15	21	16	3	3	1	68
	$M_2 = 45{\cdot}956 \pm 0{\cdot}179$									

Diff. $M_1 - M_2 = 0{\cdot}919$
$m_{diff.} = 0{\cdot}118$

The maturing and mature herring (stages III—VI) are typical Bank herring and need not be discussed here. Thus we have to deal only with the 32 herrings of maturity I—II, which showed the following length distribution:—

cm.....	23	24	25	26	27	28	Total	Average
Number..	1	6	5	11	7	2	32	25·75 cm.

The combinations of gill rakers, VS, and K_2, for each length, are given in Table 2.

Judging from Figure 1 we would expect, in the length groups concerned, GR = 44—46 in autumn spawners, and GR > 47·5 in late winter spawners. It will be seen that the variation and averages of the 25 specimens of 25 cm. and over, correspond fairly well with the late winter-spawning type, whereas the 7 specimens of 23—24 cm. are more related to the autumn-spawning type (except the VS counts, but this may be a random error).

Calculating the average values for the two length groups and their differences, these are rather small for VS and K_2, but rather large and highly significant for GR, in spite of the small number of variates. Applying the *t*-test (Goulden 1952, p. 56, formula 18), both the differences in GR and K_2 are found to be significant. Therefore the differences cannot be ascribed to the difference in growth only.

In many cases the gill-raker counts will prove sufficient for characterizing with a considerable degree of accuracy, the herring in a mixed sample. Additional counts of other meristic characters, however, will always be very useful. This has proved to be a valuable means by which to discriminate between autumn spawners and late winter spawners. On account of their geographical distribution, sexual separation, and morphological differentiation—as demonstrated by the gill rakers—we are inclined to regard these groups as two systematically well defined subspecies.

It should be mentioned that minor differences in the conventional meristic characters, VS and K_2, such as those between Bank and Downs herring, occur together with minor differences in the number of gill rakers. These more closely related herring forms may be regarded as "microsubspecies", i.e., subspecies "in statu nascendi", or merely as ecotypes. It cannot be determined statistically, but will depend rather on time, e.g. evolution, than on human experience.

Table 2

Length in cm.	23	24	25	26	27	28
GR/VS/K_2	45/57/15	42/57/16	47/57/15	46/57/13	45/58/14	47/58/15
		43/57/16	47/57/14	46/58/14	46/57/13	50/57/14
		44/57/15	47/57/14	47/58/?	47/57/14	
		44/56/13	48/58/14	48/57/14	48/57/14	
		45/57/15	48/58/14	48/57/14	48/57/13	
		46/57/14		48/57/15	49/56/14	
				48/57/13	49/57/12	
				48/57/13		
				48/57/13		
				49/56/13		
				49/58/15		
n	1	6	5	11	7	2

	M_a	m	σ_a^2
GR	$44{\cdot}143 \pm 0{\cdot}508$		1·8095
VS	$56{\cdot}857 \pm 0{\cdot}143$		0·1429
K_2	$14{\cdot}857 \pm 0{\cdot}404$		1·1429

	M_b	m	σ_b^2
GR	$47{\cdot}640 \pm 0{\cdot}230$		1·3233
VS	$57{\cdot}200 \pm 0{\cdot}115$		0·3333
K_2	$13{\cdot}792 \pm 0{\cdot}159$		0·6069

	$M_a - M_b$	$m_{diff.}$	P
GR	3·417	0·558	<0·01
VS	0·343	0·184	> 0·1
K_2	1·065	0·434	<0·01

Summary

The method of gill-raker counts is commonly used for taxonomical purposes, especially for discrimination between closely related forms of fish. This method was used by the author in racial work on herring. Only the rakers of the lower branch of the first left arch are counted.

An actual correlation between body length and number of gill rakers was found. This correlation, however, is of some importance in young herring only, but very insignificant in mature fish.

On comparing the curves of the average gill-raker numbers of Atlantic and North Sea Bank herring of equal lengths there is in general a difference of about two rakers, that is, a much greater difference than in either the average number of vertebrae or the number of keeled scales.

In many cases the gill-raker counts will prove sufficient for an individual characterization, with a considerable degree of accuracy, of the herring in a mixed sample. This method has proved to be valuable in the discrimination of autumn spawners and late winter spawners. These two groups of herring are considered as two systematically well defined subspecies.

Minor differences in other meristic characters (VS, K_2), such as are found, for example, between the Bank and the Downs herring, are combined with minor differences in gill-raker numbers. The taxonomic status of these more closely related herring tribes cannot be determined statistically.

Literature

Ginsburg, J.: "Arithmetical definition of the species, subspecies and race concept, with a proposal for modified nomenclature." Zoologica, **23**: 253—286. New York, 1938.

Goulden, C. H.: "Methods of Statistical Analysis." 2nd ed., 467 pp. New York & London, 1952.

Heincke, F.: "Naturgeschichte des Herings I." Abhandl. Dtsch. Seefischerei-Verein, **2**: I—CXXXVI and 1—128. Berlin, 1898.

Krefft, G.: "Die Zahl der Kiemenreusenfortsätze als Hilfsmittel bei morphologischen Heringsuntersuchungen." Ber. Dtsch. Wiss. Komm. Meeresforsch., **13** (4): 298—309. Stuttgart, 1954.

4.

Variation in Meristic Characters of Young Atlantic Menhaden, *Brevoortia tyrannus*

By Fred C. June

Introduction

The menhadens which inhabit the Atlantic and Gulf coastal waters of North America support the largest commercial fishery in the Western Hemisphere. In the United States they account for about one-third of the total annual fish catch. Of the four species found in these waters, the Atlantic menhaden, *Brevoortia tyrannus* (Latrobe) is most important. It is exploited from the Gulf of Maine to central Florida and accounts for an estimated 70% of the combined annual menhaden production.

This study of variation in meristic characters in young of this species was undertaken to determine whether one or more populations occur in estuarine nursery areas along the Atlantic coast. The work is part of an investigation undertaken in 1955 for purposes of determining the causes and predictability of fluctuations in menhaden abundance.

Methods

The study is based on samples of juveniles of the 1955 year-class from various nursery areas between Cape Cod and southern Georgia (Fig. 1). Fish were collected with beach seines; and, without exception, each sample represented a number of different schools.

Meristic characters selected for examination included vertebrae, ventral scutes, dorsal and left pectoral fin rays. Vertebral counts were made from X-ray photographs, except for one sample (Connecticut River) where specimens were prepared by a staining method described by Clothier (1950) prior to counting. Vertebral number included the total segments between, but not including, the basioccipital and hypural. Counts of ventral scutes and fin rays were made under a dissecting microscope. Ray counts included all rays, however small, which could be

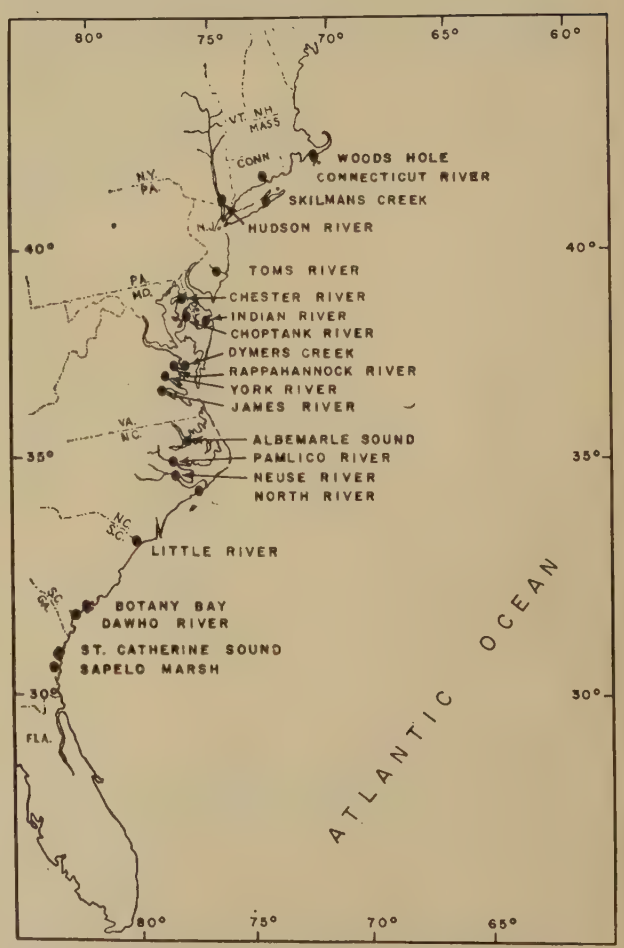


Figure 1. Map of the Atlantic coast of the United States showing the localities sampled.

Table 1
Mean numbers of vertebrae, ventral scutes, and dorsal and left pectoral fin rays in male and female juvenile menhaden from five localities along the Atlantic coast of the United States

Locality and Character	Males			Females		
	Mean	Number	$S(x-\bar{x})^2$	Mean	Number	$S(x-\bar{x})^2$
Woods Hole, Mass.:						
Vertebrae	46·66	64	14·44	46·67	86	26·88
Ventral scutes	31·73	71	37·92	31·55	88	61·82
Dorsal rays	20·93	71	28·65	21·00	88	38·00
Left pectoral rays	15·45	71	35·58	15·56	88	28·72
Skilmans Creek, N.Y.:						
Vertebrae	46·82	54	10·15	46·77	61	14·79
Ventral scutes	32·00	54	30·00	31·81	62	35·68
Dorsal rays	21·37	54	28·59	21·49	61	27·25
Left pectoral rays	15·78	54	41·33	15·66	62	27·89
Indian River, Del.:						
Vertebrae	47·00	138	40·00	47·06	138	29·54
Ventral scutes	32·54	138	102·32	32·59	138	105·46
Dorsal rays	21.66	138	52·99	21·74	138	72·61
Left pectoral rays	16·52	138	99·44	16·54	138	78·24
Neuse River, N.C.:						
Vertebrae	47·07	89	27·60	47·12	84	16·81
Ventral scutes	32·84	89	45·80	32·88	85	54·82
Dorsal rays	21·78	89	47·51	21·93	85	47·85
Left pectoral rays	16·86	64	37·74	17·00	64	24·00
Sapelo Marsh, Ga.:						
Vertebrae	47·08	40	16·78	47·15	40	13·10
Ventral scutes	33·20	39	22·36	32·90	40	43·60
Dorsal rays	21·70	40	20·40	21·56	40	17·78
Left pectoral rays	16·66	40	18·74	16·82	40	53·78

distinguished without dissection. In some cases fins were stained with alizarin and comparisons made of counts before and after staining.

Results

Variation of meristic counts with sex

To determine whether the sexes differed significantly from each other in meristic characters, preliminary comparisons were made of fish from five localities (Table 1). Analyses of these data indicated that the differences encountered could have arisen from chance variation. It was concluded that the sexes need not be segregated in comparing the meristic counts.

Variation of meristic counts with length

To test the relation between meristic number and fish size, regressions were calculated for those samples in which inspection of the data indicated a likelihood of obtaining positive results. Both positive and negative regressions resulted, and except for one sample, Skilmans Creek (Oct. 5), the regression coefficients did not differ significantly from zero. Inspection of Figure 2 shows that this sample has two modes. Comparisons of dorsal and pectoral fin-ray counts showed highly significant differences ($P < 0{\cdot}01$) between the means of modal groups, 35—64 mm. and 74—104 mm. Interpretation of these results will be discussed in a later section (p. 35). In the analyses which follow, length was not considered as a source of variation.

Number of vertebrae

Distributions of vertebral counts for individual samples and localities are given in Table 2. Vertebral number proved to be least variable of the four meristic characters examined. Counts made on 1961 fish ranged from 45 to 48, and of these, 71% had 47 vertebrae.

An analysis of variance of mean vertebral numbers in all samples, is summarized below:—

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Localities	20	63·25	3·16	10·19*)
Samples	7	2·14	0·31	1·15
Individuals	1933	518·48	0·27	

*) Highly significant; P is less than 0.01.

Comparison of the resulting variance ratio with a table of F values given in Snedecor (1946) shows highly significant heterogeneity between means for

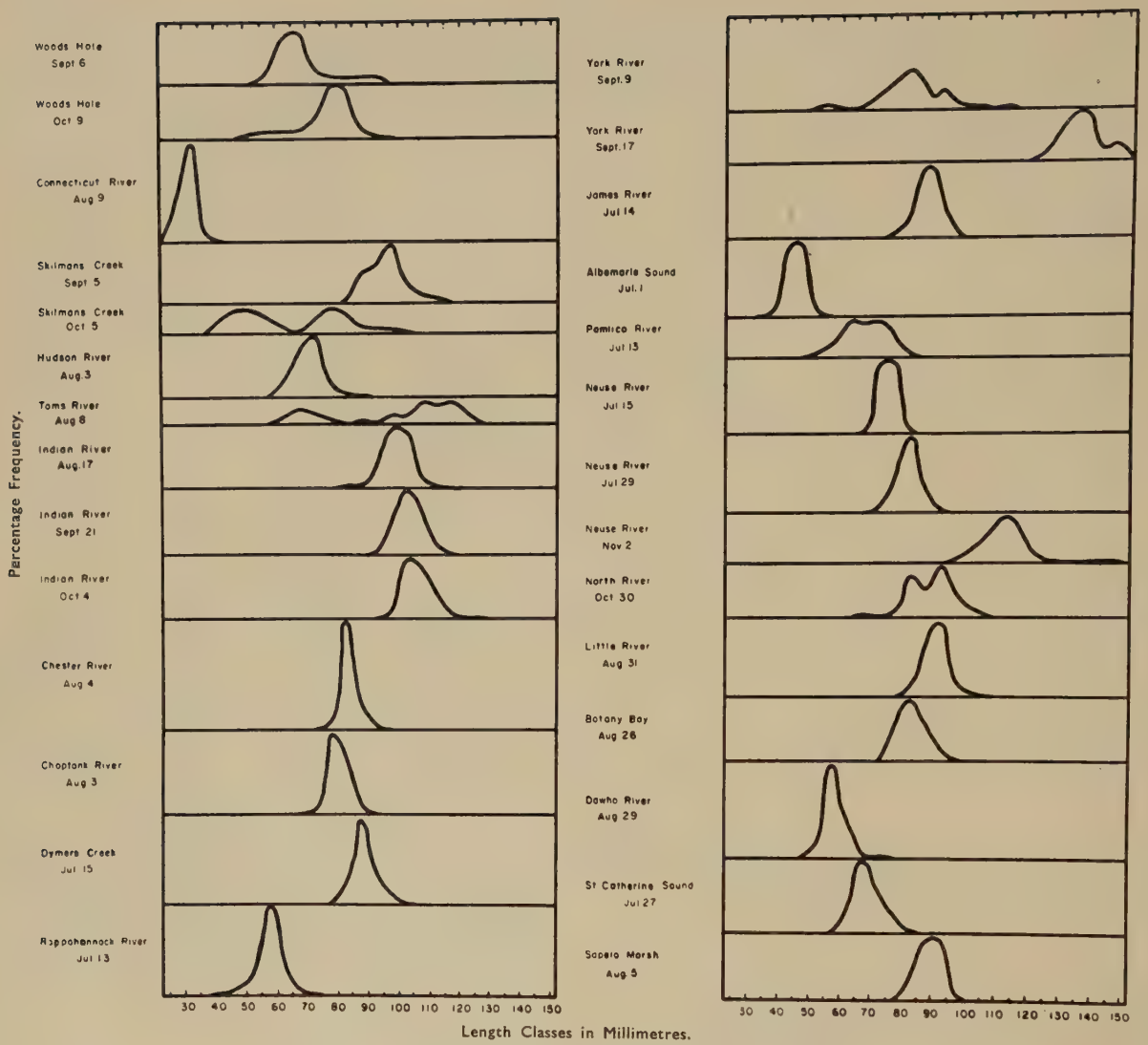

Woods Hole Sept 6
Woods Hole Oct 9
Connecticut River Aug 9
Skidmans Creek Sept 5
Skidmans Creek Oct 5
Hudson River Aug 3
Toms River Aug 8
Indian River Aug 17
Indian River Sept 21
Indian River Oct 4
Chester River Aug 4
Choptank River Aug 3
Dymers Creek Jul 15
Rappahannock River Jul 13
York River Sept 9
York River Sept 17
James River Jul 14
Albemarle Sound Jul 1
Pamlico River Jul 13
Neuse River Jul 15
Neuse River Jul 29
Neuse River Nov 2
North River Oct 30
Little River Aug 31
Botany Bay Aug 26
Dawho River Aug 29
St Catherine Sound Jul 27
Sapelo Marsh Aug 5
Percentage Frequency.
30 40 50 60 70 80 90 100 110 120 130 140 150
Length Classes in Millimetres.

Figure 2. Length frequency distributions of the samples.

localities, indicating that more than one population was represented in the samples. The analysis also demonstrates that individual samples within the several localities were drawn from a homogeneous population.

Inspection of Table 2 shows that although locality means vary irregularly, there is a distinct decrease in vertebral number north of Long Island. In view of this, analyses were undertaken separately for the area north of Long Island (northern area) and the area south of Long Island (southern area) to determine whether the samples within each area represented a homogeneous population. The results are summarized in the following tabulation:—

Area	Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Northern	Localities ..	1	1·40	1·40	6·67
	Samples ...	1	0·21	0·21	0·70
	Individuals.	207	61·35	0·30	
Southern	Localities ..	17	8·05	0·47	2·04
	Samples ...	5	1·16	0·23	0·85
	Individuals.	1585	427·62	0·27	

Resultant F values indicate no significant differences, either between samples within the same locality, or between localities within each area. The variance ratios lie well within the 5% level.

Table 2
Number of vertebrae in samples of juvenile menhaden from various nursery areas on the Atlantic coast of the United States in 1955

Locality and date	Number of fish with counts of:				Total number	Mean		
	45	46	47	48		Sample	Locality	Area
Woods Hole, Mass.:								
September 6	1	31	58	2	92	46·66		
October 9	—	30	36	2	68	46·59		
All	1	61	94	4	160	—	46·63	46·59
Connecticut River, Conn.:								
August 9	1	26	23	—	50	46·44	46·44	
Skilmans Creek, N.Y.:								
September 5	—	12	62	1	75	46·85		
October 5	—	22	44	2	68	46·71		
All	—	34	106	3	143	—	46·78	
Hudson River, N.Y.:								
August 3	—	2	43	2	47	47·00	47·00	
Toms River, N.J.:								
August 8	1	7	54	7	69	46·97	46·97	
Indian River, Del.:								
August 17	—	10	73	17	100	47·07		
September 21	—	10	34	6	50	46·92		
October 4	1	11	48	13	73	47·00		
All	1	31	155	36	223	—	47·02	
Chester River, Md.:								
August 4	—	7	64	16	87	47·10	47·10	
Choptank River, Md.:								
August 3	—	6	34	8	48	47·04	47·04	
Dymers Creek, Va.:								
July 15	—	5	40	5	50	47·00	47·00	
Rappahannock River, Va.:								
July 13	—	12	78	18	108	47·05	47·05	
York River, Va.:								
September 9	—	6	24	5	35	46·97		
September 17	—	5	50	7	62	47·03		
All	—	11	74	12	97	—	47·01	47·08
James River, Va.:								
July 14	—	5	46	12	63	47·11	47·11	
Albermarle Sound, N.C.:								
July 1	—	12	56	17	85	47·06	47·06	
Pamlico River, N.C.:								
July 13	—	1	34	16	51	47·29	47·29	
Neuse River, N.C.:								
July 15	—	6	59	10	75	47·05		
July 29	—	6	60	14	80	47·10		
November 2	—	5	55	16	76	47·14		
All		17	174	40	231	—	47·10	
North River, N.C.:								
October 30	—	2	27	6	35	47·11	47·11	
Little River, N.C.:								
August 31	—	5	60	14	79	47·11	47·11	
Botany Bay, S.C.:								
August 26	—	2	54	18	74	47·22	47·22	
Dawho River, S.C.:								
August 29	—	7	70	23	100	47·16	47·16	
St. Catherine Sound, Ga.:								
July 27	—	8	54	19	81	47·14	47·14	
Sapelo Marsh, Ga..:								
August 5	—	11	49	20	80	47·11	47·11	

Table 3

Number of ventral scutes in samples of juvenile menhaden from various nursery areas on the Atlantic coast of the United States in 1955

Locality and date	Number of fish with counts of:										Total number	Mean		
	28	29	30	31	32	33	34	35	36	37		Sample	Locality	Area
Woods Hole, Mass.:														
September 6	—	—	6	28	57	3	—	1	—	—	95	31·64		
October 9	—	1	6	30	27	9	1	—	—	—	74	31·54		
All...	—	1	12	58	84	12	1	1	—	—	169	—	31·60	31·58
Connecticut River, Conn.:														
August 9	1	–	6	16	18	9	—	—	—	—	50	31·54	31·54	
Skilmans Creek, N.Y.:														
September 5	—	1	1	17	38	17	1	—	—	—	75	31·96		
October 5	—	—	1	15	44	14	1	—	—	—	75	31·99		
All...	—	1	2	32	82	31	2	—	—	—	150	—	31·97	
Hudson River, N.Y.:														
August 3	—	—	1	3	13	23	6	—	—	—	46	32·65	32·65	
Toms River, N.J.:														
August 8	—	—	—	7	23	30	12	3	—	—	75	32·75	32·75	
Indian River, Del.:														
August 17	—	—	—	4	52	35	9	—	—	—	100	32·49		
September 21	—	—	—	4	17	24	5	—	—	—	50	32·60		
October 4	—	—	1	6	23	25	18	—	—	—	73	32·73		
All...	—	—	1	14	92	84	32	—	—	—	223	—	32·59	
Chester River, Md.:														
August 4	—	—	—	5	32	36	14	—	—	—	87	32·68	32·68	
Choptank River, Md.:														
August 3	—	—	—	5	14	22	7	—	—	—	48	32·65	32·65	
Dymers Creek, Va.:														
July 15	—	—	—	4	17	20	8	—	—	—	49	32·65	32·65	
Rappahannock River, Va.:														
July 13	—	—	—	3	38	57	17	—	—	—	115	32·77	32·77	
York River, Va.:														
September 9	—	—	—	3	6	21	6	—	—	—	36	32·83		
September 17	—	—	—	3	22	25	11	1	—	—	62	32·76		
All...	—	—	–	6	28	46	17	1	—	—	98	—	32·79	32·78
James River, Va.:														
July 14	—	—	—	3	11	28	19	2	—	—	63	33·09	33·09	
Albermarle Sound, N.C.:														
July 1	—	—	-	5	36	43	3	—	—	—	87	32·51	32·51	
Pamlico River, N.C.:														
July 13	—	—	—	2	11	31	8	1	—	1	54	32·98	32·98	
Neuse River, N.C.:														
July 15	—	—	—	—	16	45	14	—	—	—	75	32·97		
July 29	—	—	—	8	12	52	9	—	—	—	81	32·77		
November 2	—	—	—	1	16	22	11	—	—	—	50	32·86		
All...	—	—	–	9	44	119	34	—	—	—	206	—	32·86	
North River, N.C.:														
October 30	—	—	—	4	14	17	5	—	—	—	40	32·56	32·56	
Little River, N.C.:														
August 31	—	—	—	5	19	42	11	2	—	—	79	32·82	32·82	
Botany Bay, S.C.:														
August 26	—	—	—	4	18	36	16	—	—	—	74	32·86	32·86	
Dawho River, S.C.:														
August 29	–	—	—	2	27	61	9	1	—	—	100	32·80	32·80	
St. Catherine Sound, Ga.:														
July 27	—	—	—	—	17	51	18	—	—	—	86	33·01	33·01	
Sapelo Marsh, Ga.:														
August 5	—	—	—	4	13	36	23	3	—	—	79	33·10	33·10	

Finally, to determine whether each major area differed significantly from Long Island, comparisons were made of mean counts from the latter with those from each of the other two areas. The variance ratios obtained corresponded to probabilities of less than 0·01 that they belong to a common population.

Results of the foregoing analyses indicate that juvenile menhaden inhabiting Atlantic coast nursery areas are composed of at least two populations, one north and another south of Long Island. Intermingling between the two areas apparently occurs in the vicinity of Long Island.

Number of ventral scutes

Distributions of ventral scute counts in samples from the various localities are given in Table 3. Counts were made on 1978 fish and varied between 28 and 37.

An analysis of variance of the mean scute numbers for all localities is summarized in the following tabulation:—

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Localities	20	379·64	18·98	28·76*)
Samples.....	7	4·63	0·66	1·00
Individuals...	1950	1281·45	0·66	

*) Highly significant; P is less than 0.01.

The results show statistically significant heterogeneity between localities. It also will be observed that the samples within a given locality were drawn from a common population. As in the case of vertebrae, a distinct decrease in mean scute number occurs north of Long Island while no particular trend is evident southward. Accordingly, analyses were undertaken separately for the two areas with the following results:—

Area	Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Northern	Localities ..	1	0·13	0·13	0·30
	Samples ...	1	0·43	0·43	0·56
	Individuals.	216	166·63	0·77	
Southern	Localities ..	17	42·99	2·53	3·01
	Samples ...	5	4·18	0·84	1·29
	Individuals.	1586	1026·95	0·65	

These analyses gave no indication that the samples within the same locality or between localities within each area were not drawn from a homogeneous population.

Mean counts for Long Island fish were then compared with those from each of the other two areas. The resultant F values lead to the conclusions already drawn from the vertebral data, namely, that at least two population groups may be identified in the nursery areas along the Atlantic coast, (1) north of Long Island and (2) south of Long Island. Intermingling appears to take place in the vicinity of Long Island.

Number of dorsal rays

Table 4 gives the distributions of dorsal ray counts of samples from the various localities. Counts on 1979 fish ranged from 18 to 24 fin rays.

In the analysis of variance which follows, it may be seen that highly significant heterogeneity is indicated between the means of dorsal ray counts for the various localities. However, there is no contrary evidence to indicate that the samples within the several localities were not drawn from a common stock:—

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Localities	20	172·48	8·62	18·74*)
Samples.....	7	3·22	0·46	0·94
Individuals...	1951	949·28	0·49	

*) Highly significant; P is less than 0.01.

To test the probability that the northern and southern areas each contain a homogeneous population, analyses were calculated separately for the two areas with the following results:—

Area	Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Northern	Localities ..	1	1·52	1·52	0·97
	Samples ...	1	1·57	1·57	3·49
	Individuals.	216	96·26	0·45	
Southern	Localities ..	17	12·85	0·76	2·45
	Samples ...	5	1·53	0·31	0·63
	Individuals.	1588	777·92	0·49	

In neither case were the results significant, and it was concluded that there is no evidence that more than one population exists within each area. Separate comparisons of mean dorsal ray counts of samples from Long Island waters with those from each of the other two areas show similar results to those already presented for the vertebral and ventral scute data.

Number of pectoral rays

A preliminary comparison was made of the number of rays in both the right and left pectoral fins in a sample of 100 fish from Indian River, Delaware. The mean count for the left pectoral fin was 16·67 and 16.61 for the right fin. The difference of 0.06 had a standard error of 0·115. A difference of this magnitude could have arisen from chance variation. Accordingly, counts were limited to the left pectoral fin.

Table 4

Number of dorsal rays in samples of juvenile menhaden from various nursery areas on the Atlantic coast of the United States in 1955

Locality and date	Number of fish with counts of:							Total number	Mean		
	18	19	20	21	22	23	24		Sample	Locality	Area
Woods Hole, Mass.:											
September 6	—	—	26	56	12	1	—	95	20·87		
October 9	—	—	11	48	14	1	—	74	21·07		
All...	—	—	37	104	26	2	—	169	—	20·96	20·91
Connecticut River, Conn.:											
August 9	—	2	15	26	7	—	—	50	20·76	20·76	
Skilmans Creek, N.Y.:											
September 5	—	1	6	38	29	1	—	75	21·31		
October 5	—	—	7	37	26	4	—	74	21·36		
All...	—	1	13	75	55	5	—	149	—	21·34	
Hudson River, N.Y.:											
August 3	—	—	—	18	27	2	—	47	21·66	21·66	
Toms River, N.J.:											
August 8	—	—	3	32	35	5	—	75	21·56	21·56	
Indian River, Del.:											
August 17	—	—	3	30	54	13	—	100	21·77		
September 21	—	—	—	17	29	4	—	50	21·74		
October 4	—	—	4	25	32	10	1	72	21·71		
All...	—	—	7	72	115	27	1	222	—	21·74	
Chester River, Md.:											
August 4	—	—	2	19	55	11	—	87	21·86	21·86	
Choptank River, Md.:											
August 3	—	—	—	18	25	5	—	48	21·73	21·73	
Dymers Creek, Va.:											
July 15	—	—	—	10	36	4	—	50	21·88	21·88	
Rappahannock River, Va.:											
July 13	—	—	2	33	65	15	1	116	21·83	21·83	
York River, Va.:											
September 9	—	—	—	11	18	7	—	36	21·89		
September 17	—	—	1	16	38	7	—	62	21·82		
All...	—	—	1	27	56	14	—	98	—	21·85	21·77
James River, Va.:											
July 14	—	—	—	21	36	6	—	63	21·76	21·76	
Albermarle Sound, N.C.:											
July 1	—	—	1	21	52	13	—	87	21·89	21·89	
Pamlico River, N.C.:											
July 13	—	—	1	15	29	7	2	54	21·89	21·89	
Neuse River, N.C.:											
July 15	—	—	1	28	37	8	1	75	21·73		
July 29	—	—	1	23	43	13	1	81	21·88		
November 2	—	—	2	12	24	12	—	50	21·92		
All...	—	—	4	63	104	33	2	206	—	21·84	
North River, N.C.:											
October 30	—	—	—	13	22	4	1	40	21·82	21·82	
Little River, N.C.:											
August 31	—	—	1	27	44	6	1	79	21·73	21·73	
Botany Bay, S.C.:											
August 26	—	1	2	16	42	12	—	73	21·85	21·85	
Dawho River, S.C.:											
August 29	1	—	2	33	55	9	—	100	21·68	21·68	
St. Catherine Sound, Ga.:											
July 27	—	—	3	31	44	7	1	86	21·67	21·67	
Sapelo Marsh, Ga.:											
August 5	—	—	5	24	46	5	—	80	21·64	21·64	

Table 5

Number of left pectoral rays in samples of juvenile menhaden from various nursery areas on the Atlantic coast of the United States in 1955

Locality and date	Number of fish with counts of:							Total number	Mean		
	13	14	15	16	17	18	19		Sample	Locality	Area
Woods Hole, Mass.:											
September 6	—	2	47	44	2	—	—	95	15·48		
October 9	—	4	32	37	2	—	—	75	15·49		
All...	—	6	79	81	4	—	—	170	—	15·49	15·51
Connecticut River, Conn.:											
August 9	—	1	22	23	4	—	—	50	15·60	15·60	
Skilmans Creek, N.Y.:											
September 5	—	2	23	39	9	2	—	75	15·81		
October 5	1	—	21	42	11	—	—	75	15·83		
All...	1	2	44	81	20	2	—	150	—	15·82	
Hudson River, N.Y.:											
August 3	—	—	1	21	23	2	—	47	16·55	16·55	
Toms River, N.J.:											
August 8	—	—	7	32	28	6	1	74	16·49	16·49	
Indian River, Del.:											
August 17	—	—	7	44	42	7	—	100	16·49		
September 21	—	—	2	21	24	3	—	50	16·56		
October 4	—	—	6	39	23	3	2	73	16·40		
All...	—	—	15	104	89	13	2	223	—	16·48	
Chester River, Md.:											
August 4	—	—	2	28	47	8	2	87	16·77	16·77	
Choptank River, Md.:											
August 3	—	—	—	20	23	25	—	48	16·69	16·69	
Dymers Creek, Va.:											
July 15	—	—	1	14	29	3	2	49	16·82	16·82	
Rappahannock River, Va.:											
July 13	—	—	4	25	66	21	—	116	16·90	16·90	
York River, Va.:											
September 9	—	—	1	14	18	3	—	36	16·64		
September 17	—	1	2	19	34	6	—	62	16·68		
All...	—	1	3	33	52	9	—	98	—	16·66	16·65
James River, Va.:											
July 14	—	—	6	24	28	5	—	63	16·51	16·51	
Albemarle Sound, N.C.:											
July 1	1	—	5	30	41	9	1	87	16·62	16·62	
Pamlico River, N.C.:											
July 13	—	—	1	19	28	6	—	54	16·72	16·72	
Neuse River, N.C.:											
July 15	—	—	2	25	41	7	—	75	16·71		
July 29	—	—	—	21	50	10	—	81	16·86		
November 2	—	—	1	11	31	7	—	50	16·88		
All...	—	—	3	57	122	24	—	206	—	16·81	
North River, N.C.:											
October 30	—	—	3	12	21	4	—	40	16·65	16·65	
Little River, N.C.:											
August 30	—	1	3	32	37	5	1	79	16·57	16·57	
Botany Bay, S.C.:											
August 26	—	—	1	30	37	6	—	74	16·65	16·65	
Dawho River, S.C.:											
August 29	—	—	5	42	45	6	—	98	16·53	16·53	
St. Catherine Sound, Ga.:											
July 27	—	—	2	34	42	8	—	86	16·65	16·65	
Sapelo Marsh, Ga.:											
August 5	—	—	4	33	36	7	—	80	16·56	16·56	

Distributions of the left pectoral ray counts of 1979 fish from the various localities are given in Table 5. Analysis of the data was undertaken with the following results:—

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Localities	20	343·81	17·19	57·30*)
Samples.....	7	2·13	0·30	0·58
Individuals...	1951	1009·45	0·52	

*) Highly significant; P is less than 0.01.

As in the previous analyses of vertebral, ventral scute, and dorsal ray data, there were no differences between the means for samples from the same locality; however, the means for various localities along the coast show significant heterogeneity. Inspection of Table 5 indicates that the samples from the northern area are responsible for a major part of the large variance between localities.

The following analyses gave no indication that the samples within the northern and southern areas, considered separately, were not drawn from a homogeneous population:—

Area	Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Northern	Localities ..	1	0·4826	0·4826	137·89
	Samples ...	1	0·0035	0·0035	0·01
	Individuals.	217	84.4730	0·3893	
Southern	Localities ..	17	28·23	1·66	3·86
	Samples ...	5	2·13	0·43	0·81
	Individuals.	1586	840·83	0·53	

Finally, comparisons of the mean number of pectoral rays in Long Island specimens with those of each of the other two areas showed significant differences between means.

Discussion

A consideration of meristic characters in juvenile menhaden of the 1955 year-class demonstrated more than one population in various nursery areas between Cape Cod and Florida. Consistent differences in mean numbers of vertebrae, ventral scutes, and dorsal and pectoral rays indicated at least two populations, one occurring north of Long Island and another south of Long Island.

It has been accepted generally that variation in the number of metameric parts in fishes results from variation in environmental conditions, notably temperature, during early development (Vladykov, 1934; Tåning, 1952; Lindsey, 1954). In several clupeoid species, for example, there appears to be an inverse relation between the average number of meristic characters and water temperature (Rounsefell and Dahlgren, 1932; Tester, 1938; McHugh, 1942, 1951). The possibility that the observed differences

Table 6. Mean monthly water temperatures at certain Atlantic coast stations (°F.)

Location and date	Temperature	Locality Mean	Area Mean
Myrtle Beach, S. C.			
November 1954...	59·9		
December – ...	50·5		
January 1955...	50·0	53·9	
February – ...	50·0		
March – ...	59·3		
			49·0
Kiptopeke Beach, Va.			
November 1954...	52·9		
December – ...	42·2		
January 1955...	39·7	44·0	
February – ...	38·3		
March – ...	46·8		
New London, Conn.			
May 1955...	60·2		
June – ...	64·9	62·6	
			60·1
Woods Hole, Mass.			
May 1955...	53·1		
June – ...	62·2	57·6	

in meristic counts of juvenile menhaden may have been induced by water temperature during the time of spawning and early larval development, therefore, was investigated.

Before examining the relation between meristic data and water temperature it is necessary to examine our sketchy knowledge of the time and location of menhaden spawning. Based on the examination of gonads of many thousands of fish over the entire range of the fishery in 1955, together with the results of plankton surveys for eggs and larvae, it appears that a major spawning occurs off the coast of the Carolinas from November through March. In waters north of Long Island, on the other hand, spawning appears to be confined to a relatively short period in early summer. These conclusions, of course, do not preclude the possibility that spawning occurs along the entire coast.

These findings agree in general with the progressively later spawning toward the north, noted for other clupeoid fishes, e.g., for Pacific herring, *Clupea pallasii* (Rounsefell, 1930) and Pacific sardine, *Sardinops caerulea* (Clark and Marr, 1955).

In Table 6 are given the only available water temperatures for those areas where spawning is presumed to occur during particular months. I am indebted to Mr. Robert W. Knox of the U.S. Coast and Geodetic Survey who furnished these data.

Inspection of the table indicates a difference of about 11° F. between mean temperature from November to March in the vicinity of the Carolinas and the early summer temperature north of Long Island. It also should be noted, however, that this difference is less than the average difference between the maximum in November and the minimum in February (about 12° F.) in waters off the Carolinas. Nevertheless, it seems reasonable to conclude from these data that

an inverse relation between water temperature and mean meristic number obtains for Atlantic menhaden. Further investigation, especially of the distribution of eggs and larvae in the ocean, is needed before the times and places of spawning can be determined with greater reliability.

Whether the observed differences in meristic characters also may be due to genetic factors cannot be determined in the light of present knowledge. Whatever the cause, the data presented show that populations of juvenile fish inhabiting Atlantic coast estuaries do not intermingle completely. Mean counts of vertebrae, ventral scutes, and dorsal and pectoral fin rays remain relatively constant along the great length of coast between Georgia and southern Long Island, then suddenly decrease in the area northward. It will be recalled (p. 27) that significant differences were noted for dorsal and pectoral ray counts between the two size groups represented in the Long Island sample (Skilmans Creek — Oct. 5). Comparisons of the mean counts for the two size groups with those of juveniles in the areas north and south of Long Island suggest that young of both the southern and northern spawnings are represented in this sample. Indeed, it would be expected that intermingling should take place in those waters if the hypotheses regarding the time and places of spawning are correct. Further evidence concerning the extent of intermingling, movements of young following their migration to sea, and the relation between the times and places of occurrence of spawning adults and resulting year broods must await future work, preferably the results of tagging experiments.

Summary

The Atlantic menhaden, *Brevoortia tyrannus* (Latrobe), occurs in the coastal waters of North America from the Gulf of Maine to central Florida and is the object of an intensive fishery over most of this range.

A study of variation in meristic characters in young of this species was undertaken to determine whether one or more populations inhabit the estuarine nursery areas. Material examined consisted of samples of juveniles of the 1955 year-class collected from 21 different localities between Cape Cod and southern Georgia. Four meristic characters were selected for study: vertebrae, ventral scutes, dorsal fin rays, and left pectoral fin rays. Vertebral counts were made from X-ray photographs and stained specimens and included the total number of segments between, but not including, the basioccipital and hypural bones. Fin ray counts included all rays, however small, that could be seen without dissection.

Preliminary studies indicated that mean counts of the various characters do not vary with sex. It also was concluded that, in general, meristic counts are not related to the length of the fish over the size range represented (28 to 150 mm. fork length). Finally, no difference was noted in the mean number of rays in the right and left pectoral fins.

Analyses of variance applied to the meristic data gave no evidence of significant heterogeneity between the means of successive samples taken in the same locality. There was significant heterogeneity between the means for localities. Further analyses indicated that at least two populations of juveniles inhabit the estuarine nursery areas, one occurring north of Long Island and another south of Long Island. Intermingling between the two areas apparently occurs in the vicinity of Long Island. A distinct decrease in the mean counts of all characters in the area north of Long Island was noted. It is concluded that the difference in mean water temperatures during the time of spawning and early larval development may be sufficient to induce the observed differences in mean meristic counts between the two areas.

Acknowledgements

I gratefully acknowledge the assistance of Mr. Doyle F. Sutherland who carefully and assiduously performed most of the meristic counts on which this study is based. Dr. Earl E. Deubler, now associated with the North Carolina Institute of Fisheries Research, assisted in the collection of samples and performed some of the preliminary counts.

References

Clark, F. N., & J. C. Marr, 1955. "Population dynamics of the Pacific sardine." Part II in Progress Report: California Cooperative Oceanic Fisheries Investigations, 1 July 1953—31 March 1955, pp. 21—48, Sacramento.

Clothier, Ch. R., 1950. "A key to some southern California fishes based on vertebral characters." California Div. Fish & Game, Fish Bull., 79, 83 pp.

Lindsey, C. C., 1954. "Temperature-controlled meristic variation in the paradise fish *Macropodus opercularis* (L.)." Can. J. Zool., **32** (2): 87—98.

McHugh, J. L., 1942. "Vertebral number of young herring in southern British Columbia." J. Fish. Res. Bd. Canada, **5** (5): 474—84.

— 1951. "Meristic variations and populations of northern anchovy (*Engraulis mordax mordax*)." Scripps Inst. Oceanogr. Bull., **6** (3): 123—60.

Rounsefell, G. A., 1930. "Contribution to the biology of the Pacific herring, *Clupea pallasii*, and the condition of the fishery in Alaska." U. S. Bur. Fish., Fish. Doc., 1080: 227—320.

Rounsefell, G. A., & E. H. Dahlgren, 1932. "Fluctuations in the supply of herring, *Clupea pallasii*, in Prince William Sound, Alaska." U. S. Bur. Fish., Bull., 9: 263—91.

Snedecor, George W., 1946. "Statistical methods applied to experiments in agriculture and biology." Iowa State Coll. Press, 4th Ed., xvi + 485 pp., Ames, Iowa.

Tåning, Å. Vedel, 1952. "Experimental study of meristic characters in fishes." Biol. Rev. Cambridge Phil. Soc., **27**: 169—93.

Tester, A. L., 1938. "Variation in the mean vertebral count of herring (*Clupea pallasii*) with water temperature." J. Cons. Int. Explor. Mer, **13** (1): 71—75.

Vladykov, V. D., 1934. "Environment and taxonomic characters of fishes." Trans. Roy. Can. Inst., **20**: 99—140.

5.

The Tribes in the North Coast Herring of Iceland with Special Referenc to the Period 1948–1955

By Árni Friðriksson

Introduction

The herring fishing off the north coast of Iceland is almost entirely limited to July and August. The fishing area is located off the north coast, but, in some years, a considerable part of the catches comes from the north-east coast and some 30—40 years ago the north-west coast area was also of considerable value. The herring consist almost exclusively of spring spawners of a very large size and high age (averages about 35 cm. and 11—12 years).

The greatest part of the catches is normally processed for herring meal and oil, but a considerable part is cured for human consumption or frozen for bait. Since the thirties, when the processing came to full development, the annual yields may indicate bad or good fishing years. There have been two periods, the one, 1930—1945, with good, the other, 1945—1955, with poor yields. As far as is known 1956 seems to represent a turning point towards better yields again.

There have been different views as to the origin of the north coast herring, as will be mentioned in the following discussion.

Earlier investigations

It is well known that Heincke considered the Icelandic herring as a particular race, distinctly separated from the large Norwegian spring herring (Heincke, 1898). It is, however, to be remembered that his material comprised only 24 full-grown specimens from an unknown place of capture and with an unknown spawning time.

Sæmundsson was the first to point out that there are two herring races in Icelandic waters, a spring spawning and a summer spawning one (Sæmundsson, 1906).

During 1919—1927 Johansen published four papers about the Icelandic herring. In his paper of 1926 he gives the following summary of the average number of vertebrae (VS) in the samples he had investigated (Johansen, 1926):—

Spring spawning herring

Locality	Date	Year	Number	Av. number of VS
S. Coast	Spring	1924–25	84	57·49 ± 0·08
—	14.IX	1924	11	57·55 ± ?
N. Coast	22.VII	1924	143	57·48 ± 0·07
—	12.IX	1924	49	57·49 ± 0·08

Summer spawning herring

Locality	Date	Year	Number	Av. number of VS
S.W. Coast ...	14.V	1919	297	57·07 ± 0·04
— ...	14.VIII	1919	180	57·01 ± 0·05
N.W. Coast ...	6.IX	1924	36	57·08 ± ?
N. Coast	Sept.	1915	31	57·00 ± ?
—	12.IX	1924	47	56·98 ± 0·09

Johansen comes to the conclusion that there are two (and only two) races of herring in the Icelandic waters and that the spring spawning herring is an independant stock, very similar to the large herring of the west coast of Norway. He admits that there may be interchanges between the stocks. However, he finds that the spawning places of the north coast spring spawners are situated at the south and south-west coast of Iceland, in the "warm area" (Johansen, 1927).

In his paper of 1936, Runnström comes to exactly the same conclusions as Johansen with respect to the Icelandic spring spawning herring. He finds that "the Icelandic and the Norwegian spring herrings are closely related forms which cannot be separated by their body characters. But investigations of the age and growth seem to indicate that one can divide them geographically and that they inhabit different areas in the same manner as the Icelandic and the Norwegian cod" (Runnström, 1936).

Runnström's material originates from the years 1929—35, mainly from 1931—33. The average number of VS, etc. runs as follows:—

Adult spring spawning herring

Locality	Date	Year	Number	Av. number of VS
S.W. Coast...	February	1933	66	57·20 ± 0·06
N. Coast.....	21.VII	1931	140	57·17 ± 0·04
—	22.VII-29.VIII	1932	1102	57·12 ± 0·02
—	July(?)	1933	136	57·15 ± 0·05

Adult summer spawning herring

S.W. Coast...	May	1932	181	56·96 ± 0·04
N. Coast.....	22.VII-29.VIII	1932	44	57·00 ± 0·11
—	July(?)	1933	45	56·96 ± 0·09

It is very interesting to note that the average number of VS has declined considerably from the twenties to the thirties.

The period 1937-1942

This period is dealt with in a paper published by the author in 1944 (Friðriksson, 1944). But before considering the results of the vertebrae countings some introductory remarks must be made.

In the spring of 1935 (and 1936) an attempt was made to spot the spawning localities of the spring spawning herring. As the result of this experiment was entirely negative it was concluded that the great stock of the north coast spring herring did not spawn off the south coast of Iceland. Further consideration led to the theory that this stock must be much more closely linked with the spring spawning herring of Norway than was assumed earlier, and that the greatest part of it was bound to spawn in Norwegian waters and migrate to the north coast of Iceland, where it remained during the summer months (Friðriksson, 1935). As we have seen neither Johansen nor Runnström were able to find any definite difference between the VS value in the spring spawners of north and south Iceland. We must, however, keep in mind that their material from the south coast was rather poor, consisting of 95 (Johansen) and 206 fish (Runnström) only. Furthermore, a negative proof is no definite proof, and, finally, the south coast herring investigated by Runnström diverges considerably from that of the north coast.

In the summer of 1939 the few (6) north coast herring at stage II had a very high number of vertebrae (57·333) as compared with the main bulk of the spring spawners. The same feature was observed regarding the I-stage herring in 1941 and 1942. The identity of this small fraction of the stock was not realized at that time, but it was found advisable to classify it separately as b spring spawners in order to separate them from the main bulk of spring herring, the a-group. Bearing this classification in mind the average number of VS during 1937—42 can be summarized as follows:—

VS	Spring spawners Type a	Spring spawners Type b	Summer spawners
60.....	4	—	—
59.....	113	3	—
58.....	3432	25	33
57.....	11427	24	136
56.....	2603	3	38
55.....	71	—	2
54.....	20	—	—
53.....	3	—	—
N	17673	55	209
M	57·05	57·51	56·96
± m.....	0·01	0·09	0·04

It is also of interest to compare the average number of VS in all Icelandic herring during this period as is done by the following figures:—

Spring Spawners	Number	Av. number of VS
S. Coast.....	222	57·17 ± 0·04
N. Coast (Type a)...	17673	57·05 ± 0·01
— (Type b)...	55	57·51 ± 0·09
Summer Spawners		
S.W. Coast	1688	56·98 ± 0·02
N. Coast	209	56·96 ± 0·04

If we now calculate the standard deviation of the differences for VS by the formula

$$\frac{M_1 - M_2}{\sqrt{m_1^2 + m_2^2}}$$

where M_1 and M_2 are the average numbers of VS and m_1 and m_2 the standard deviations of the means of the two tribes compared, we arrive at the figures given in Table 1.

Table 1
Standard deviations of the differences for VS

Locality	Type of herring	S.and S.W.Coast Sum. spawn.	S.and S.W.Coast Spr. spawn.	N. Coast Sum. spawn.	N. Coast Spr. spawn.b
N. Coast ...	Spr. sp. a	6·8	3·0	2·2	5·0
— ...	— b	5·7	3·3	5·4	—
— ...	Sum. spawn.	0·5	3·7	—	—
S. and S.W. Coast..	Spr. spawn.	4·4	—	—	—

The conclusions from this comparison are that:—

1. The greater part of the north coast spring spawners (Type a) is significantly different from the spring spawning herring of the south coast, from the b type of the north coast, from the summer spawners of the south coast and very different from the summer spawners found off the north coast.

2. The b type shows significant differences from all other herring.

3. The summer spawners of the south seem to be identical with those of the north.

4. The spring spawners and the summer spawners of the south are significantly different.

The most important of these conclusions is that the

spring spawners of the south and south-west coast on one hand, and those of the north coast on the other, seem to be significantly different.

It is of great interest to note the very big decrease in the average number of VS during the short period in question (1924—1942). As regards the north coast spring spawning herring, the decline appears from this comparison:—

Johansen	1924	$57{\cdot}48 \pm 0{\cdot}07$	(n = 143)
Runnström	1933	$57{\cdot}12 \pm 0{\cdot}02$	(n = 1102)
Friðriksson ...	1938–42	$57{\cdot}05 \pm 0{\cdot}01$	(n = 17673)

The variation from year to year during 1938—42 was found to be rather small:—

1938	$57{\cdot}03 \pm 0{\cdot}01$	(4482)
1939	$57{\cdot}05 \pm 0{\cdot}01$	(4852)
1940	$57{\cdot}07 \pm 0{\cdot}01$	(3749)
1941	$57{\cdot}08 \pm 0{\cdot}01$	(2127)
1942	$57{\cdot}04 \pm 0{\cdot}01$	(2463)

It is, however, worth to note that the value of VS increases until 1941, when it drops again.

The period 1948-1955

This period was characterized by very poor yields, in spite of much better equipment to spot the herring than ever before. During this period large-scale marking experiments were introduced both in Iceland and Norway. As the results of the marking experiments have a close bearing on the racial question, a brief survey of the Icelandic taggings and the resulting returns in Norway is given in Table 2. The percentage of returns in Norway range, as can be seen from the table, between 0·7 (1948) and 5·1 (1953).

It must be pointed out that during 1948—1955 only 414 tagged north coast herring were returned from Iceland, all from the banks of the north coast. It appears, therefore, that the number of returns from Norway is about 5 times greater than those from Iceland.

During 1953—55, 10,400 herring were tagged off the S. and S.W. coasts of Iceland. Some local returns have been reported, and one from Norway. A herring tagged on 21. August 1953 at Gardskagi, S.W. Iceland, was caught off the west coast of Norway in the spring of 1955. Detailed information as to locality and date of recapture is not yet available. It is worth mentioning that none of the herrings tagged off south and south-west Iceland have been returned from the north coast and no north coast herrings have as yet been reported from the south coast.

From the great number of herring which have been liberated from the west coast of Norway, only 15 tags have been found in the factories on the north coast of Iceland during 1949—55. These poor returns may, perhaps, partly be explained through the nearly entire failure of the herring at north Iceland during the period in question. It is also interesting to note that the percentage number of returns from Iceland on the Norwegian fishing grounds are much higher than those of herring tagged in Norwegian waters. It sounds paradoxical that the herring of the north coast of Iceland is more Norwegian than the Norwegian herring itself.

From the facts revealed through the tagging experiments we come to the very important conclusion that in 1949—1956 the major spawning of the north coast herring has taken place at Norway.

The Tribes in the North Coast Herring

Since 1948 an effort has been made to analyse the north coast herring as to the elements by which it is composed. This has been done by means of the structure of the scales. There have been found four "tribes":—

1. Norwegian spring spawners, northern type.
2. Norwegian spring spawners, southern type.
3. Icelandic spring spawners, and
4. Icelandic summer spawners.

It has been found out that the so-called spring spawning Type b, mentioned earlier, must be considered as Icelandic spring spawners with an extremely high total number of vertebrae.

Table 2
Number of north coast herring tagged and number of returns from Norway

Year of tagging	Number tagged	Number of returns in Norway								Total
		1949	1950	1951	1952	1953	1954	1955	1956	
1948	7,475	1	11	7	9	9	12	1	1	51
1949	0	—	—	—	—	—	—	—	—	—
1950	1,321	—	—	10	15	8	12	4	4	53
1951	3,064	—	—	—	30	34	56	19	15	154
1952	17,308	—	—	—	—	262	340	132	103	837
1953	10,181	—	—	—	—	—	300	110	110	520
1954	8,783	—	—	—	—	—	—	121	70	191
1955	9,241	—	—	—	—	—	—	—	146	146
1956	8,450	—	—	—	—	—	—	—	—	—
Total	65,823	1	11	17	54	313	720	387	449	1,952

Table 3
The relative strength of tribes during 1948-1955 (‰)

Year	Norway N. type	Norway S. type	Iceland Spr. sp.	Iceland Sum. sp.	Total	Uncertain as to tribe	Total Number
1948	578	110	282	30	1000	314	3,932
1949	737	210	53	0	1000	375	3,683
1950	654	285	42	19	1000	47	2,599
1951	628	202	140	30	1000	219	2,600
1952	666	156	94	84	1000	157	1,969
1953	565	175	171	89	1000	534	3,931
1954	412	160	391	37	1000	271	2,094
1955	413	169	396	22	1000	380	3,196
Average	582	183	196	39	1000		24,004

In Table 3 a survey is given of the relative strength of the tribes in the north coast herring during the period in question. It is evident that the Norwegian spring spawning herring (large and spring herring) has been dominating the whole period, comprising more than three quarters of the total catch on an average (765‰). It has ranged in strength from 572‰ in 1954 to 947‰ in 1949, by number. As this herring is much older and larger than the Icelandic herring found off the north coast, it has of course contributed still more by weight.

It also appears from the table that the Icelandic summer spawners never play any important role off the north coast. They have only contributed by 4% on an average and even less when their small size, as compared with the Norwegian herring, and their poor quality is considered. Through the years 1952—1954 the relative number of the north Norwegian herring decreased from year to year at the same time as the Icelandic spring spawners were increasing in number. This development seems to have stopped in 1955, but it is too early to say if a turning point has been reached.

The Age of the North Coast Herring by Tribes

In Figures 1 to 4 the age composition of the tribes from year to year is shown. A glance at Figure 1 reveals that there have been two strong dominating year-broods during the period, the broods from 1934 and 1937, in the northern Norwegian herring. There are some other good broods and during recent years the brood from 1943 has shown signs of relative predominance.

As to the southern Norwegian herring (Figure 2) we find the 1934 brood absolutely dominating in 1948, and relatively strong through 1949—1953, but the 1937 brood is not very important. Other good broods are those from 1940, 1943, 1944, and 1947.

It is worth to note that the broods from 1934, 1937, 1943, 1944, and 1947 have been predominant in the spring and large herring catches at Norway during the same years (Devold, 1951—56).

Turning to the Icelandic spring spawners (Figure 3) we find the 1944 brood good in 1948—51, 1945 is a dominant from 1950, and 1949 seems to have been very strong since 1953. The year-brood from 1940 appears in 1951 and 1952, and there is trace of the broods from 1937 in 1949, and from 1934 in 1949 and 1950. The predominance of the broods from 1944, 1945, and 1949 is in conformity with the results of Einarsson (1955).

Finally, in the summer spawning stock only one year-brood has been predominant off the north coast during recent years, that of 1945 (6 rings in the scales in 1951, etc.). Other year-classes have appeared here rather sporadically, but it must be kept in mind that the material on which the investigations are based is rather scanty.

Table 4
Average age composition of the tribes during 1948-1955 (‰)

Age years	N. Norway type	S. Norway type	Iceland spr. spawn.	Iceland sum. spawn.
2	—	—	2	—
3	—	+	49	11
4	1	3	**179**	**78**
5	2	15	**184**	**164**
6	6	40	**160**	**124**
7	12	67	**74**	**104**
8	18	**97**	**80**	**231**
9	23	**121**	**98**	**130**
10	43	**120**	**108**	40
11	71	**125**	19	38
12	**100**	**101**	17	22
13	**97**	74	10	13
14	**152**	74	6	14
15	**160**	61	9	14
16	**127**	45	4	11
17	**86**	32	1	3
18	53	12	+	2
19	29	9	+	—
20	14	4	—	1
21	6	+	—	—
22	+	—	—	—
23	+	+	—	—
24	+	—	—	—
Total	1000	1000	1000	1000
N	12,923	3,908	4,527	875
Mean age	14·1	11·1	6·7	7·6

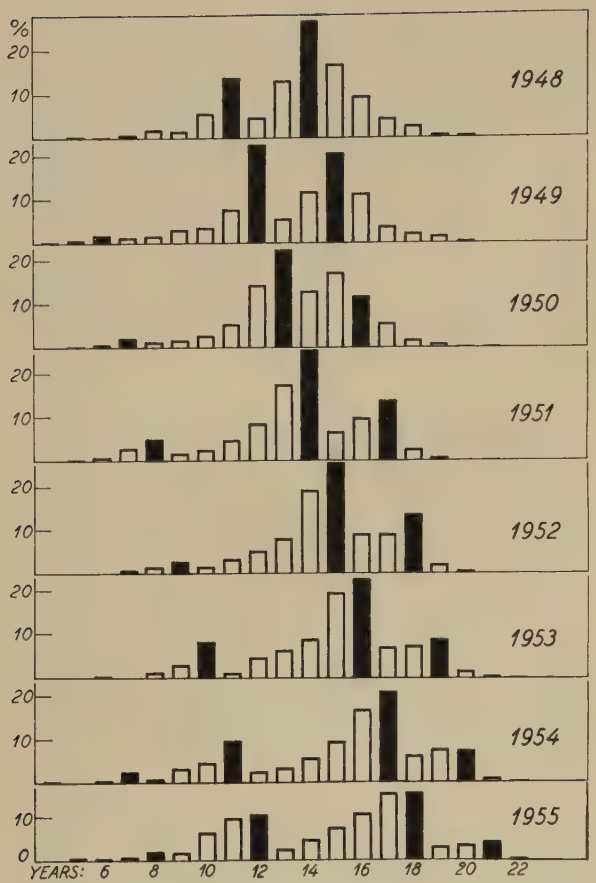


Figure 1. Norwegian spring spawners, northern type.

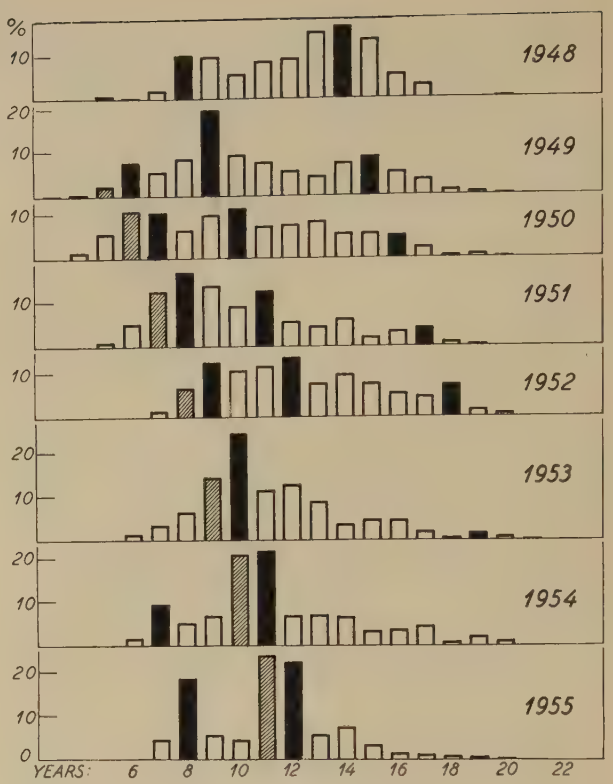


Figure 2. Norwegian spring spawners, southern type.

Before leaving the age distribution it is of interest to consider the average composition of the tribes for the whole period 1948—1955. A survey is given in Table 4.

The great differences as to age are rather striking and can be summarized as follows:—

1. Northern Norwegian herring, average age 14·1 years, range 12—17 years (722‰).
2. Southern Norwegian herring, average age 11·1 years, range 8—12 years (564‰).
3. Icelandic spring spawners, average age 6·7 years, range 4—10 years (883‰).
4. Icelandic summer spawners, average age 7·6 years, range 4—9 years (831‰).

The Total Number of Vertebrae (VS)

As may be seen from Table 5 the total number of vertebrae has varied a great deal, not only from tribe to tribe but also from year to year within the same tribe. An over-all tendency to increased number of vertebrae during the period will be noted. The number of fish, examined annually as to VS value, ranged between 995—2513 and 278—723 for the two Norwegian tribes, and between 67—1152 and 25—306 for the Icelandic ones. The relatively low number in the Icelandic spring spawners in 1950 is based on few countings (67) and the same applies to the summer spawners of 1950, which show a high figure (34 fish).

If we summarize the number of vertebrae as is done in Table 6, where the distribution is also shown, we come to the conclusion that there is no remarkable difference between the northern and the southern Norwegian types of spring spawners, whereas there is a considerable difference between these on one

Table 5
Averages of total number of vertebrae

Year	N. Norway	S. Norway	Iceland spr. spawn.	Iceland sum. spawn.
1948.....	57·10	57·06	57·10	56·52
1949.....	57·17	57·24	57·20	56·73
1950.....	57·11	57·06	56·85	57·12
1951.....	57·11	57·08	57·06	56·85
1952.....	57·18	57·12	57·15	56·90
1953.....	57·17	57·19	57·16	57·03
1954.....	57·18	57·14	57·24	57·09
1955.....	57·19	57·29	57·22	56·93

Table 6
Average number of VS for the whole period 1948-1955 (‰)

VS	Spring spawners N. Norway	S. Norway	Iceland	Total	Sum. spawn.	Grand Total
60.....	+	—	—	+	—	+
59.....	11	13	12	12	9	12
58.....	256	260	267	260	165	255
57.....	609	592	609	604	626	605
56.....	120	131	105	119	191	123
55.....	4	4	7	5	9	5
54.....	+	+	+	+	—	+
53.....	+	—	—	+	—	+
Total	1000	1000	1000	1000	1000	1000
N	12293	3908	4527	20728	1037	21765
M	57·15	57·15	57·17	57·15	56·98	57·14
± m.....	0·01	0·01	0·01	0·01	0·02	0·01

hand and the Icelandic spring spawners on the other. The summer spawners are significantly separated from all other herring by their lower number of vertebrae.

In Tables 7—10 surveys have been made of the VS values of the particular broods, partly from year to year, and partly through the whole period. The number of fish investigated is indicated by the figures below the average values. In cases when only few fish represent a brood in a particular year they are omitted from the table.

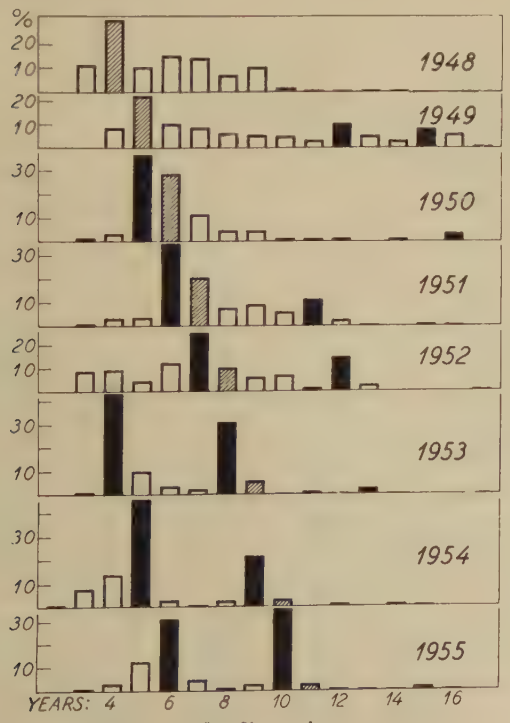


Figure 3. Icelandic spring spawners.

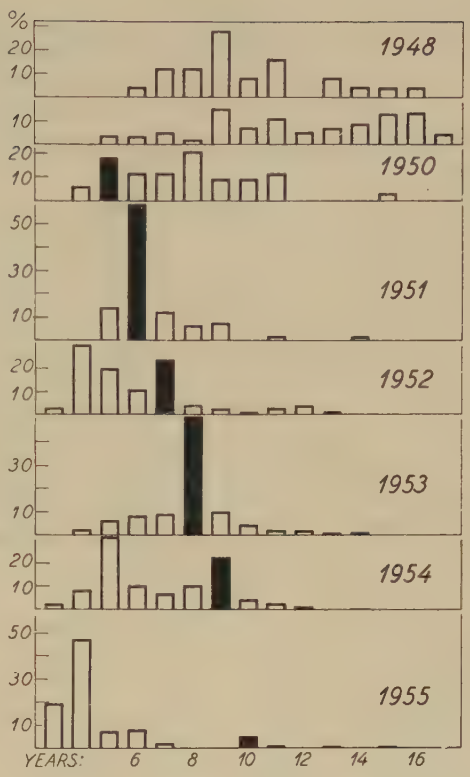


Figure 4. Icelandic summer spawners.

Table 7, which deals with the northern Norwegian herring, is based on much better material than any other of the tables. We see, however, that the average VS of the same brood may vary considerably from one year to another. If we consider, for instance, the strong 1937 year-brood, we find that the range of variation is from 57·066 (in 1949) to 57·224 (in 1954). A glance at the last column of this table reveals, however, that there has been a tendency to increasing number of vertebrae from the earliest brood (1931) to the broods of 1938 and 1939, when a maximum of 57·201 was reached, followed by a small, but nearly continous decrease from brood to brood as far as the material reaches.

The picture as regards the southern Norwegian herring (Table 8) is not so clear, and the material is not very representative, but an increasing number of vertebrae from about the beginning of the thirties to the middle of the forties is indicated.

A comparison between the broods of the Icelandic spring spawning herring is hardly possible owing to too few observations (Table 9). An increasing tendency from about 1940 to 1950 seems to be suggested.

For the summer spawning herring of Iceland (Table 10) there are very few observations from the north coast, and, of course, no general conclusions can be made. But it is interesting to note that from 1944 there seems to be a definite trend downwards, exactly

Table 7
Average values of VS by year-broods (Northern Norwegian type)
N = number of fish in each year

Year-Brood	Year of capture								Total
	1948	1949	1950	1951	1952	1953	1954	1955	
1931 VS	56·977	57·121	—	—	—	—	—	—	57·098
N	86	52	—	—	—	—	—	—	138
1932 VS	57·130	57·045	—	—	—	—	—	—	57·088
N	192	99	—	—	—	—	—	—	291
1933 VS	57·034	57·217	57·068	—	—	—	—	—	57·106
N	350	292	73	—	—	—	—	—	715
1934 VS	57·137	57·185	57·065	57·071	57·159	57·098	57·193	—	57·130
N	560	515	154	198	145	153	83	—	1,808
1935 VS	57·090	57·120	57·072	57·158	57·206	57·194	57·035	—	57·125
N	266	319	222	139	97	124	85	—	1,252
1936 VS	57·032	57·234	57·103	57·137	57·135	57·195	57·132	—	57·137
N	93	133	165	95	96	118	68	—	768
1937 VS	57·143	57·066	57·112	57·135	57·187	57·183	57·224	57·212	57·158
N	281	573	287	364	272	394	237	156	2,564
1938 VS	57·155	57·293	57·087	57·077	57·196	57·178	57·242	57·178	57·201
N	116	196	183	247	204	343	190	152	1,631
1939 VS	—	57·068	57·232	57·077	57·116	57·203	57·286	57·226	57·201
N	—	82	69	117	86	148	105	106	713
1940 VS	—	—	—	57·234	57·111	57·262	57·109	57·263	57·192
N	—	—	—	64	54	107	64	76	365
1941 VS	—	—	—	—	—	57·187	57·105	57·184	57·155
N	—	—	—	—	—	80	38	49	167
1942 VS	—	—	—	—	—	—	57·208	57·074	57·141
N	—	—	—	—	—	—	24	27	51
1943 VS	—	—	—	—	—	—	57·113	57·212	57·162
N	—	—	—	—	—	—	106	104	210
1944 VS	—	—	—	—	—	—	—	57·153	57·153
N	—	—	—	—	—	—	—	98	98
1945 VS	—	—	—	—	—	—	—	57·138	57·138
N	—	—	—	—	—	—	—	65	65

Table 9
Average values of VS by year-broods (Icelandic spring spawners)
N = number of fish in each year

Year-Brood	Year of capture								Total
	1948	1949	1950	1951	1952	1953	1954	1955	
1939 VS	57·153	57·438	—	—	—	—	—	—	57·295
N	98	16	—	—	—	—	—	—	114
1940 VS	57·147	57·222	—	56·964	—	—	—	—	57·111
N	68	18	—	28	—	—	—	—	114
1941 VS	57·014	56·800	—	57·067	—	—	—	—	56·960
N	140	25	—	15	—	—	—	—	180
1942 VS	56·975	57·143	—	56·955	57·364	—	—	—	57·109
N	158	28	—	22	11	—	—	—	219
1943 VS	56·971	57·313	—	57·105	—	—	—	57·182	57·143
N	102	67	—	19	—	—	—	11	199
1944 VS	57·247	57·320	56·789	57·075	57·133	57·088	57·154	57·032	57·105
N	312	25	19	53	15	34	26	31	515
1945 VS	57·051	—	56·920	57·089	57·150	57·230	57·171	57·204	57·116
N	118	—	25	90	40	200	199	406	1,078
1946 VS	—	—	—	—	57·263	57·231	57·097	57·048	57·160
N	—	—	—	—	19	13	21	63	116
1947 VS	—	—	—	—	—	57·043	—	57·353	57·198
N	—	—	—	—	—	23	—	17	40
1948 VS	—	—	—	—	56·600	57·113	57·294	57·082	57·022
N	—	—	—	—	15	62	34	49	160
1949 VS	—	—	—	—	57·214	57·171	57·309	57·261	57·239
N	—	—	—	—	14	285	415	352	1,066
1950 VS	—	—	—	—	—	—	57·344	57·324	57·334
N	—	—	—	—	—	—	125	145	270
1951 VS	—	—	—	—	—	—	56·986	57·189	57·088
N	—	—	—	—	—	—	72	37	109

Table 8
Average values of VS by year-broods (Southern Norwegian type)

N = number of fish in each year

Year-Brood	Year of capture 1948	1949	1950	1951	1952	1953	1954	1955	Total
1933 VS	57·018	57·167	—	—	—	—	—	—	57·092
N	54	42	—	—	—	—	—	—	96
1934 VS	57·092	57·141	56·931	56·800	57·000	—	—	—	56·997
N	65	64	29	20	20	—	—	—	198
1935 VS	57·017	57·185	57·000	56·556	56·692	—	—	—	56·890
N	60	54	33	18	13	—	—	—	178
1936 VS	57·028	57·121	57·030	56·800	57·200	—	—	—	57·030
N	36	33	33	10	15	—	—	—	127
1937 VS	57·030	57·048	57·083	57·310	57·143	57·222	57·111	—	57·135
N	33	42	48	29	21	27	18	—	218
1938 VS	57·304	57·070	57·045	57·000	57·074	56·963	56·867	—	57·046
N	23	57	44	22	27	27	15	—	215
1939 VS	57·128	57·380	56·951	56·964	57·227	57·000	57·071	—	57·103
N	39	66	41	28	22	22	13	—	231
1940 VS	57·225	57·433	56·984	57·213	57·079	57·118	57·240	57·187	57·185
N	40	141	65	61	38	51	25	16	437
1941 VS	—	57·153	57·211	56·977	57·219	57·297	57·000	57·278	57·162
N	—	59	57	43	32	74	27	36	328
1942 VS	—	57·150	57·194	57·000	57·310	57·164	57·192	57·214	57·175
N	—	40	36	66	29	67	26	28	292
1943 VS	—	57·263	57·083	57·185	57·059	57·152	57·212	57·160	57·159
N	—	57	60	81	34	145	85	106	568
1944 VS	—	—	57·033	57·183	57·278	57·373	57·037	57·202	57·184
N	—	—	61	60	18	83	82	114	418
1945 VS	—	—	57·029	57·250	—	57·278	57·333	57·571	57·292
N	—	—	34	24	—	36	27	21	142
1946 VS	—	—	—	—	—	57·316	57·100	57·214	57·210
N	—	—	—	—	—	19	20	28	67
1947 VS	—	—	—	—	—	—	57·189	57·103	57·146
N	—	—	—	—	—	—	37	87	124

Table 10
Average values of VS by year-broods (Icelandic summer spawners)

N = number of fish in each year

Year-Broods	Year of capture 1951	1952	1953	1954	1955	Total
1943 VS	—	—	57·071	—	—	57·071
N	—	—	14	—	—	14
1944 VS	—	—	57·067	57·182	—	57·124
N	—	—	30	11	—	41
1945 VS	56·923	57·033	57·013	57·287	—	57·064
N	39	30	157	57	—	283
1946 VS	—	57·000	56·926	57·080	—	57·002
N	—	13	27	25	—	65
1947 VS	—	56·880	57·120	57·000	—	57·000
N		25	25	16		66
1948 VS	—	56·842	57·053	56·880	—	56·927
N	—	38	19	25	—	82
1949 VS	—	—	—	57·134	56·923	57·028
N	—	—	—	82	13	95
1950 VS	—	—	—	57·048	56·917	56·983
N	—	—	—	21	12	33
1951 VS	—	—	—	—	56·902	56·902
N	—	—	—	—	92	92
1952 VS	—	—	—	—	56·871	56·871
N		—	—	—	31	31

Table 11
Comparison of VS from 1919 to 1948-1955

	Reference	S. and S.W. Coast			North Coast		
		Year	N	VS	Year	N	VS
Spring spawners	Johansen	1924—25	84	57·49 ± 0·08	1924	143	57·48 ± 0·07
	Runnström	1933	66	57·20 ± 0·06	1932	1,102	57·12 ± 0·02
	Friðriksson	1938—42	222	57·17 ± 0·04	1938—48	17,673	57·05 ± 0·01
	Einarsson	1950	3,736	57·23 ± 0·01	..	..	..
	Friðriksson	..	..	..	1948—55	20,728	57·15 ± 0·01
Summer spawners	Johansen	1919	297	57·07 ± 0·04	1924	47	56·98 ± 0·07
	Runnström	1932	181	56·96 ± 0·04	1932	44	57·00 ± 0·11
	—	..	..	..	1933	45	56·96 ± 0·09
	Friðriksson	1938—42	1,688	56·98 ± 0·02	1938—42	209	56·96 ± 0·04
	Einarsson	1950	1,768	56·94 ± 0·01	..	..	..
	Friðriksson	..	..	..	1948—55	1,037	56·98 ± 0·02

contrary to the developments in the other tribes. This can perhaps be correlated with relatively high summer temperatures in coastal waters, and, as a consequence thereof, relatively poor yield of herring at the north coast during July and August.

Conclusions

If the VS is compared from period to period as is done in Table 11 it appears that both the spring spawning herring of the north coast and that of the south coast showed declining tendency until 1938—1942, but since then there has been an increasing trend. In the summer spawning herring the number of VS seems to have been rather stable. Fluctuations as to VS by broods are shown in Tables 7—10.

The spring spawning herring of the north coast has, at least during recent years, shown significant differences from that of the south and south-west coasts.

The main spawning of the north coast spring spawners seems to take place off Norway.

There is a connexion between the spring spawners at the south coast on one hand and those at the north coast and western Norway on the other.

As the northern and the southern Norwegian spring spawners can hardly be considered as different races, there appear three races of herring in the waters round Iceland:— 1, the north coast Norwegian herring; 2, the Icelandic spring spawning herring, and 3, the summer spawning herring. Perhaps these three units could quite as well be defined as tribes.

References

Devold, F., 1951, 1953, 1954, 1956. Ann. Biol., Copenhague, **7**: 125; **9**: 167; **10**: 147; **11**: 118.

Einarsson, H., 1951. Ann. Biol., Copenhague, **7**: 120.

— 1955. "Um aldursflokka i sunnansíld árin 1949—1955". Ægir, Reykjavík.

Friðiksson, Á., 1935. "Tilraunir til síldveiða á varðskipinu þor vorið 1935." Ægir, Reykjavík.

— 1944. "Norðurlands-síldin". (The herring of the north coast of Iceland). Rit Fiskideildar, 1944, (1). Siglufjord.

— 1950—1956. Ann. Biol., Copenhague, **6**: 162; **7**: 122; **8**: 136; **9**: 164; **10**: 143; **11**: 114; **12**: 158.

— 1955. "Tagging of herring in Icelandic waters." Rapp. et Proc.-Verb., **140** (2): 16—18. Copenhague.

— & Aasen, O., 1950. "The Norwegian-Icelandic herring tagging experiments. 1." Rep. Norw. Fish. Mar. Invest., **9** (11). Bergen.

— — 1952. "The Norwegian-Icelandic herring tagging experiments. 2." Rit Fiskideildar, 1951, (2). Reykjavík.

Heincke, F., 1898. "Naturgeschichte des Herings." Abh. Dtsch. SeefischVer., **2**.

Johansen, A. C., 1919. "On the large spring-spawning sea herring (*Clupea harengus* L.) in the north-west European waters." Medd. Komm. Havunders., Ser. Fisk., **5** (8). København.

— 1921. "On the summer-spawning herring (*Clupea harengus* L.) of Iceland." Ibid., **6** (3).

— 1926. "Investigations on Icelandic herrings in 1924 and 1925." Rapp. et Proc.-Verb., **39**: 114—38. Copenhague.

— 1927. "On the migrations of the herring." J. Cons. Int. Explor. Mer, **2** (1): 3—27.

Runnström, S., 1933. "Über die Rassenverhältnisse bei dem norwegischen Frühjahrshering mit besonderer Berücksichtigung der Konstanz der Rassenmerkmale." J. Cons. Int. Explor. Mer, **8** (2): 235—49. Copenhague.

— 1936. "A study of the life-history and migrations of the Norwegian spring herring based on the analyses of the winter rings and summer zones in the scales." Rep. Norw. Fish. Invest., **5** (2). Bergen.

— 1936. "Investigations on Icelandic herrings in 1929—1935." Rapp. et Proc.-Verb., **99** (4). Copenhague.

Sæmundsson, B., 1906. "Fiskirannsoknir 1905". Andvari, **31**. Reykjavík.

6.

The Icelandic Herring and Racial Problems

By Hermann Einarsson

Introduction

In spite of very different views on the division of the herring into races, biologists have with remarkable tenacity retained Heincke's main principles of division. Heincke (1898) considered races synonymous with spawning communities (Laichgemeinschaften) endowed with certain heriditary morphological and biological characters. However, during recent years experimental work has shown that the meristic characters (i.e., the morphological criteria) examined by Heincke and later workers, are oecophenotypical phenomena which makes one of the main premises invalid.

When these criteria failed in this respect emphasis was laid on the biological difference, manifested in different spawning periods or spawning localities. This was considered a physiological hereditary character of the spawning communities, which were divided into winter, spring, summer, and autumn spawners.

As regards the North Sea herring, Krefft (1955) has summarized some of the main discussions on this matter. He points out a serious difficulty in accepting this view when he states (l.c., p. 145):—

"Zunächst muss gegen die Überwertung des physiologischen Moments eingewendet werden, dass *eine Subspeziesbildung allein auf Grund einer getrennten Fortpflanzungszeit bisher in keinen Fall als erwiesen betrachtet werden kann.*[1]) Gewiss ist eine Trennung der Laichzeiten ein schwerwiegendes Moment, dass zweifellos geeignet erscheint, eine genotypische Sonderung hervorzurufen, doch *müssen wir nach unseren heutigen Kenntnissen eine solche physiologische Sonderung als etwas Sekundäres ansehen*[1]), dem weitgehende morphologische wie biologische Differenzierungen vorausgegangen sein müssen".

[1]) Author's italics.

Although Krefft thus realizes this difficulty, his schematic division of the North Sea herring (l.c., p. 151) is partly based on the principle of spawning communities or Laichgemeinschaften (Spätwinterlaicher, Herbstlaicher and Frühjahrlaicher). On the other hand it seems to me that the reliability of both principles on which Heincke based his racial division has been overestimated, and that in the light of this knowledge our approach to the problem must be reconsidered.

Seasonal communities of the Icelandic herring

Two spawning communities only inhabit Icelandic waters. Conditions are therefore much simpler than in the North Sea. This is the reason why our investigations may contribute to a better understanding of the taxonomic rank of the spawning communities.

The main differences between the Icelandic spawning communities can be summarized under 4 headings:—

1. Different spawning seasons. Spring spawners propagate mainly from the middle of March to the middle of April, summer spawners mainly from the beginning of July to the beginning of August.
2. Different nucleus characteristics of the otoliths, which have been used in the analysis of the populations (Einarsson, 1951).
3. Different degree of development of the gonads during certain periods.
4. Statistically significant differences are found in the average number of VS.

To all these characteristics we must make reservations when assessing their value as racial criteria.

To 1. A sporadic and limited spawning seems to occur outside the spawning season proper. I have

found newly hatched fry in June, and Friðriksson and Timmermann (1951) recorded herring eggs from the stomachs of haddock in the middle of May.

To 2. Although I find the nucleus characteristics the most reliable and useable feature when analysing a mixed population, these are certainly not inherited traits. Probably they owe their presence to different nourishment conditions during post-larval life.

Unfortunately our collections are not derived from every month of the year, but mainly from the period June to December. During the months October to December these characteristics show satisfactory agreement with the respective degrees of gonad development. However, during spring, in April and May, I have encountered otolith samples which did not show this agreement. It is thought that this may be due to the fact that spring spawners mix with summer spawners and *vice versa*. When more material is available from these months it is hoped that a closer analysis of this feature can be carried out.

To 3. If an interchange between spawning communities occurs, as already surmised, degree of gonad development is obviously not a reliable racial criterium. Furthermore, during the period middle of July to October, a considerable percentage of both communities remain in maturity stage VIII (recovering spents) or II (immature), and it is also difficult to distinguish between these two stages.

I strongly suspect that uncritical use of this feature as a distinguishing characteristic has often resulted in erroneous and misleading averages of meristic characters examined.

To 4. Of the meristic characters, I have especially studied the number of VS. Our statistical analysis of VS-data has shown: a) that statistically significant differences are found between spring spawners and summer spawners, taken as groups; b) that statistically significant differences are found between year-classes of the same spawning community, and c) that year-classes of spring spawners with a low average number of VS do not show significant differences from year-classes of summer spawners with a high average number of VS.

A survey of the frequency and percentage frequency of the vertebral numbers of the two respective Icelandic communities is given below:—

Number of VS	Spring spawners		Summer spawners	
	No.	%	No.	%
60	1	0·01	2	0·02
59	173	1·28	34	0·29
58	4,262	31·65	1,520	13·14
57	7,820	58·08	7,768	67·13
56	1,163	8·64	2,175	18·80
55	43	0·32	67	0·58
54	3	0·02	5	0·04
Total	13,465	100·00	11,571	100·00
M	57.249		56.937	

This table shows, firstly, that the range of the vertebral numbers is exactly the same; secondly, that the difference is only a slight shifting in the relative frequency of VS numbers.

As proved experimentally (Tåning, 1944), this shifting is primarily caused by differing temperature conditions during early embryonic life, and we must assume that the genetic basis is identical producing similar frequencies of VS at the same temperature. This, I suppose, could now be verified experimentally by rearing experiments.

In addition to these remarks some common features of the two communities can be pointed out.

1. Both communities propagate on the same spawning grounds, even the main centres of spawning activity seem to be located in the same areas.
2. During the first year the juvenile stocks mix, and subsequently the herring shoals most frequently constitute a varying mixture of both communities.
3. The growth of spring and summer spawners is identical, the summer spawners retaining their avanced growth prior to the formation of the first winter-ring until 10 years old.
4. Certain regularities in the strength of year-classes have been observed.
5. Parallellism in the average VS-number of year-classes has also been observed.[1])

These considerations lead to the conclusion that the Icelandic spawning communities of herring cannot be regarded as genetically different units, i.e., sub-species or races. In my opinion the differences are only of micro sub-specific or tribal value, from a taxonomic point of view.

The sub-species of the Atlantic herring

It is of paramount importance to keep in mind the concept of the sub-species, or geographical race, which are considered synonymous. As to this concept I wholly agree with Krefft (l.c., p. 145), when he writes:—

"Sicher ist . . ., dass der Terminus "Rasse" in der Zoologie nur für infraspezifische genotypisch einheitliche und gegen andere, in sich ebenfalls genotypisch einheitliche Einheiten innerhalb der gleichen Spezies oder des gleichen Rassenkreises morphologisch und (oder) physiologisch abgegrenzte Einheiten verwandt werden sollte. Dass es dabei zum Wesen der geographischen Rasse gehört, in den Grenzbezirken Übergänge zu zeigen, die zumindest teilweise durch Bastardisierung entstehen, sei nachdrücklich betont".

Therefore, if we acknowledge the definition of the sub-species, our first question when studying the racial problems of the herring should be: Do genotypical units exist in the stock of herring of the North Atlantic?

[1]) With regard to points 4 and 5 my previous conclusions (Einarsson, 1952) will be reconsidered in the light of more complete data and improved statistical treatment.

A. Solid line = herring of the southern North Sea and the English Channel. (After ANCELLIN).
Stipled line = autumn spawners of the North Sea caught in the Skagerak. (After ANDERSSON).
(From SAHRHAGE in KREFFT, SCHUBERT & SAHRHAGE, 1955).
B. Icelandic summer spawners.

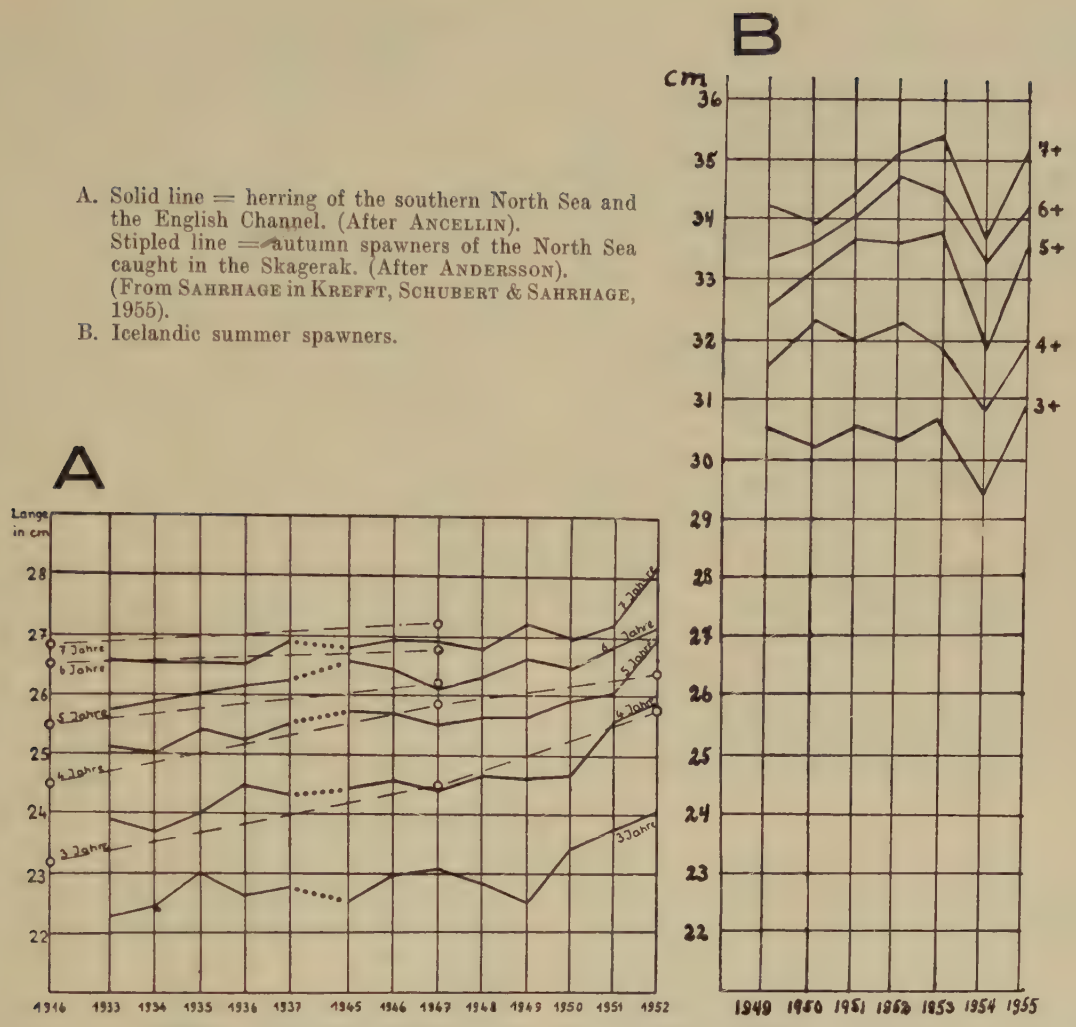


Figure 1. Comparison between average size of North Sea autumn spawning and Icelandic summer spawning herring.

I am inclined to answer this question in the affirmative, although I reject the principles on which racial division of the herring (spawning time and meristic characters) has hitherto been based. However, I am fully aware of the fact that dividing criteria are both few and inadequate, but it seems to me that some evidence is available which enables us to distinguish two sub-species of the Atlantic herring. These sub-species are:—

1. The shallow-water or North Sea herring — *Clupea harengus harengus.*
2. The oceanic or Atlantic herring — *Clupea harengus oceanicus*[1]).

[1]) As the third sub-species of the herring we must consider *Clupea harengus pallasii* of the Northern Pacific.

My reasons for considering these groups different genotypical units are the following:—

Firstly, the *different rate of growth*, viz., the *size*, of North Sea herring and Atlantic herring. This must be considered both a morphological and physiological characteristic. Ample evidence supports the conclusion that the Atlantic herring is larger at any age of its life after the first year. If the size was a phenotypical character only, we would encounter in the North Sea stock herring of the same size as the Atlantic herring, especially during years when feeding conditions are favourable. Also, we would encounter transitional rates of growth as experienced in other species common to the North Sea and the Northern Atlantic. This size difference is most marked in the mature stocks and the ultimate size.

A comparison between sizes of North Sea autumn spawners and Icelandic summer spawners is given in Figure 1.

Secondly, *different inherited migratory trends. C. harengus oceanicus* is an oceanic form, only visiting shallow waters during the spawning season. Its migrations extend far into the ocean during the greater part of the year. We are just beginning to trace these migrations by the investigations of Danish, Icelandic, and Norwegian research ships and marking experiments. *C. harengus harengus* inhabits the shelf waters during its course of life, as far as we know.

Thirdly, *the frequency of vertebral numbers.* If the genetical base is different in these two alleged sub-species, the same temperature stimulus would produce different frequencies of vertebral numbers. It is very probable that *C. harengus harengus* has a lower range and lower averages. It would be extremely interesting to test this character experimentally by rearing. On the other hand the different spawning communities of the same sub-species should show the same range and similar frequencies of vertebral numbers at the same hatching temperature.

Although inadequate, these criteria may prove a starting point in the investigation of these differences.

This division has at least the advantage that it is in accordance with the basic principle that two geographical races do not inhabit the same area, although some interbreeding may take place in the boundary zones as presupposed in the definition of the geographical race.

The micro sub-species or tribes of the herring

The ability to form micro sub-species, seasonal races or tribes must be considered a specific character of *C. harengus* as both Atlantic sub-species show this characteristic. Another common trait could be the tendency to form small-sized local populations or micro sub-species in coastal waters.

The coastal micro sub-species of *C. harengus harengus* could be the brackish water populations in coastal areas of the North Sea and of *C. harengus oceanicus*, the fjord populations of Norway (Lusterfjord, etc.).

We thus arrive at the following schematic division of the Atlantic herring:—

1. Sub-species: *C. harengus harengus.*
   (a) Micro sub-species — winter and spring spawners. Scottish coasts, the Baltic.
   (b) Micro sub-species — autumn spawners. Bank herring and Downs herring.
   (c) Micro sub-species — coastal populations in brackish waters, adjacent to the North Sea.

2. Sub-species: *C. harengus harengus.*
   (a) Micro sub-species — winter and spring spawners. Norwegian spring herring[1]), Icelandic spring herring, Viking Bank herring.
   (b) Micro sub-species — summer spawners. Icelandic summer herring, W. Greenland summer herring.
   (c) Micro sub-species — local fjord populations in Norwegian fjords.

The mixing and interchange of the tribes of *C. harengus oceanicus*

The geographical boundaries of the two sub-species lie in the northernmost North Sea and Skagerak. Although herring tagged in S.W. Norway has been recaptured in the central North Sea, the mixing of the sub-species must be conisdered of small dimensions only. These herring may even have belonged to a small contingent of North Sea herring which have exceptionally been noticed in the Norwegian stock (Rasmussen, 1939). A mixing of any significance would directly be detected in both areas by the resulting different size and age distributions of the samples.

On the other hand there is reason to expect extensive tribal interchange and mixing inside the geographical areas of the two respective sub-species. I will now consider this question as regards the oceanic herring.

The credit for having pointed out the possibility of transatlantic migrations goes to Friðriksson (1944), and the marking experiments initiated by him in 1947 have very strikingly confirmed his belief in large-scale migrations between Iceland and Norway.

A problem of great importance for future investigations of the tribes of the oceanic herring is the method of distinction. As regards the Icelandic tribes *inter se* this problem has been solved, but reliable distinguishing characteristics of Norwegian and Icelandic spring spawners have not been established to my knowledge.

The fisheries on the oceanic herring have mainly been carried out in three areas.[2]) I will now consider the mixing of tribes in each of these areas. These areas are:— 1) the S.W. Icelandic waters, 2) the north and east Icelandic waters, and 3) the Norwegian waters.

1. S.W. Icelandic waters. Outside the spawning season the Icelandic tribes are usually thoroughly mixed in this area. It was observed that similar percentage frequencies of the two tribes were repeatedly encountered. It is thought that the shoaling

[1]) Some evidence is, I believe, available regarding great variations in the onset af spawning of the Norwegian herring, and, as Devold suggests, shifting of the place of spawning. This may be due to an inherent ability of the herring to change the maturing cycle, and consequently Devold's assumptions are not as far-fetched as Andersson (1956) is led to believe and which he rejects offhand (l. c., p. 6).

[2]) The fourth area, the open Norwegian Sea, has recently been successfully exploited by Norwegian and Russian drifters.

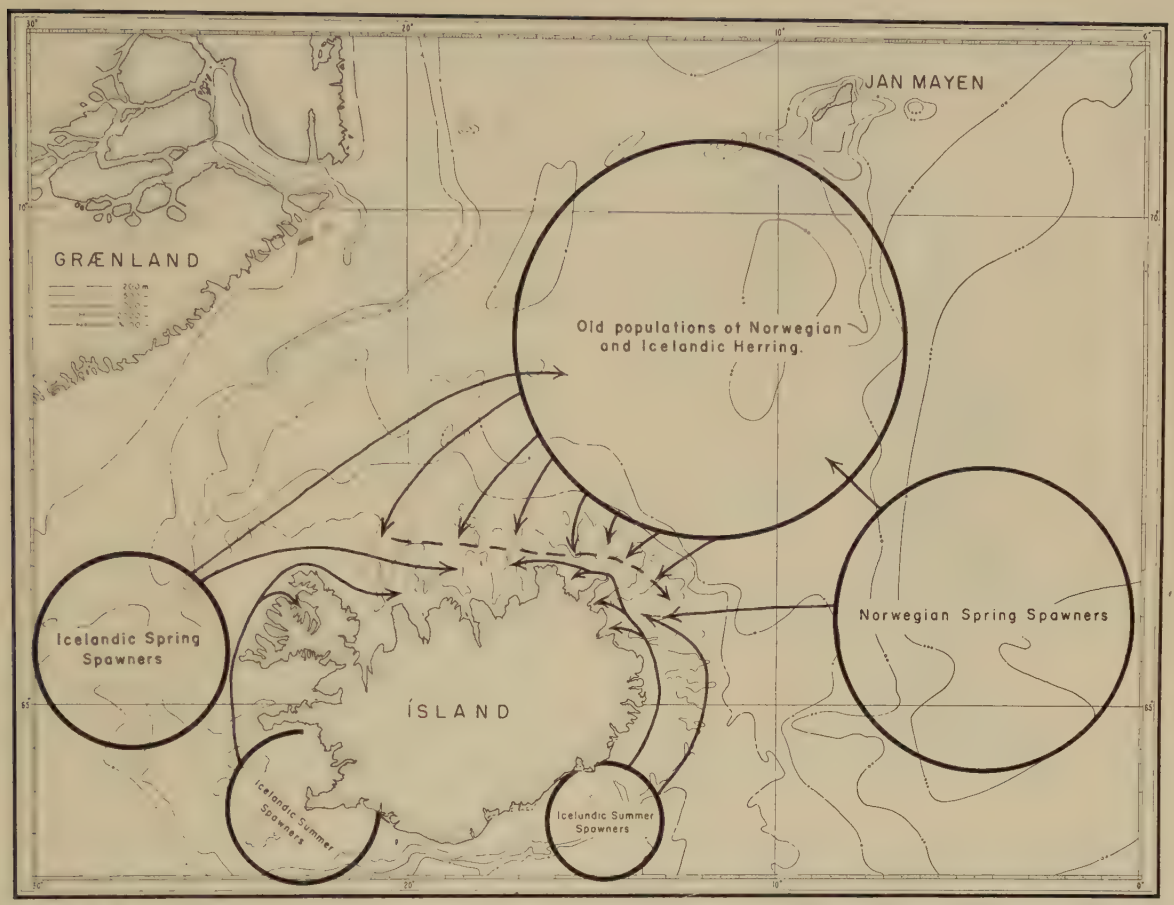


Figure 2. A schematic picture of the migrations during summer of the oceanic herring to fishing grounds off North and East Iceland.

behaviour of the herring may account for this phenomenon, which deserves a closer study.

Admixtures of extraneous herrings, e.g., of Norwegian origin, have hitherto not been observed in the S.W. Icelandic populations. On the contrary, these populations show independent traits to a marked degree. In the relative strength of year-classes there are clear differences between the Icelandic and Norwegian tribes.

Devold's hypothesis (Devold, 1955) that the Norwegian herring migrates south of Iceland and then along the west coast to appear off the north coast at the beginning of the summer season, cannot be substantiated by any observations in Icelandic waters. It is certainly a well known fact that during earlier years the influx of herring occurred from the N.W. coast waters. However, it has not been definitely established that these herring were of Norwegian origin. Furthermore, observations which I have made during the summer of 1956 indicate in fact that the Norwegian element approaches the coast from the north, as originally postulated by Friðriksson (1944).

2. The north and east Icelandic waters. These waters are rich grazing areas for the three tribes of the oceanic herring considered here. The varying degree in which the tribes are represented periodically and even annually, has caused some confusion and diverging opinions on the recruitment of this "stock".

The asdic surveys which we have made during the past 3 seasons, together with Friðriksson's investigations on the tribal composition of the "stock", lead me to consider the north and east coast herring as a composite mixture of three tribes of the oceanic herring, i. e., Icelandic spring and summer spawners and Norwegian spring spawners. The broad features of the migrations can be schematically depicted as shown in Figure 2, but much is yet to be learned about details of the migrations.

During June we have found great quantities of small herring shoals in the Iceland Sea. This spring (1956) we were fortunate enough to be able to locate larger shoals than previously encountered and in greater quantities, and we could definitely establish that these shoals migrated through the cold water

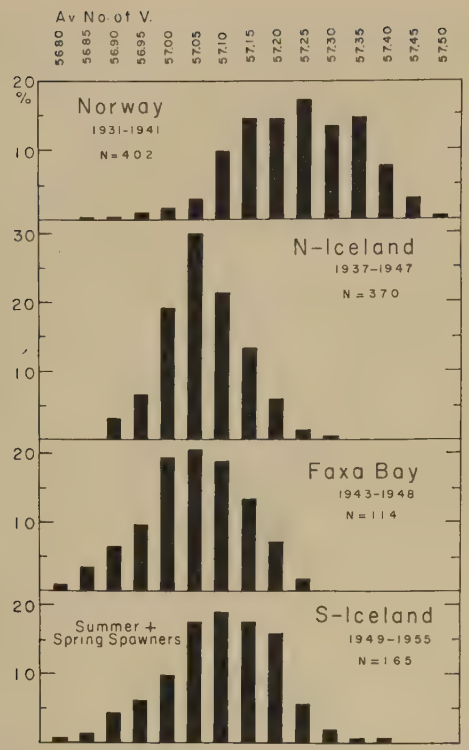


Figure 3. Percentage frequency of average vertebral numbers in samples of Norwegian and Icelandic herring.

tongue between Langanes and Jan Mayen. When these shoals reach the boundaries between colder and warmer water off the north coast they seem to coalesce into larger shoals, but apparently they do not wander far from the discontinuity layer. These herring are mainly of Norwegian origin with a small admixture of Icelandic spring spawners and consist predominantly of older year-classes. During last year's poor herring seasons this component has been dominant as shown by Friðriksson. It is very probable that these herrings constituted the large-sized "western" herring of earlier years. However, during the past two years the Icelandic component has been relatively increasing.

During the summer of 1956 another migration was observed off the N.E. coast which principally consisted of summer spawners, some of which were recently spent. This migration gave rise to an extensive fishery south of Langanes and in Vopnafjord.

The migrations from the west coast have been of little importance during recent years, but were undoubtedly of far greater magnitude in earlier years.

The evidence of vertebral numbers

Dr. Árni Friðriksson and Mr. Finn Devold have been kind enough to make available for me vertebral counts of the north Icelandic and Norwegian herring from the years 1937—1947 and 1931—1941 respec-

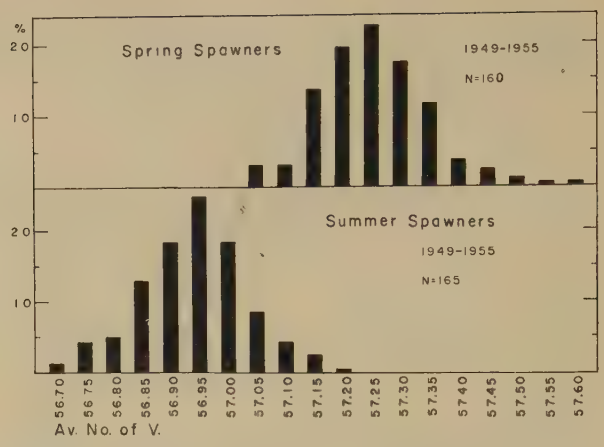


Figure 4. Percentage frequency of average vertebral numbers in samples of Icelandic spring and summer spawners.

tively. These two periods contain a number of the same year-classes, as the north Icelandic herring is considerably older than the Norwegian herring, and thus they are comparable.

For comparison I have used the mean vertebral number of samples, which usually contain 100 specimens or more. The vertebral numbers are classified into categories covering an interval of 0·050 vertebrae. For instance, all mean vertebral numbers between 56·975 and 57·025 are classified as 57·00, etc. The percentage frequency of each category was then calculated. Samples of south Icelandic herring have been treated in the same way.

Figure 3 shows the result of this effort. The dissimilarity between the Norwegian and the north Icelandic herring is so striking that the identity of the two stocks of herring during the periods mentioned must be excluded. The Norwegian herring has generally much higher mean vertebral number than the north Icelandic herring.

On the other hand, a comparison between the north Icelandic and south Icelandic herring shows an evident similarity. However, this is no proof of the hypothesis that these stocks are identical, for the following reason: both Icelandic and Norwegian spring spawners have approximately the same mean vertebral number, about 57·25.

During the period 1949—1955 I have been able to analyse the south Icelandic herring as to race by means of the otoliths (Einarsson, 1951). The average vertebral numbers of the two respective races have been treated as discussed above, and the result is shown in Figure 4. It will be seen that graphs of the south Icelandic herring in Figure 3 are the result of variable mixtures of spring spawners and summer spawners. The difference between the graphs for the periods 1943—1948 and 1949—1955 lies simply in the fact that more spring spawners were caught during the latter period.

Neither Norwegian nor Icelandic spring spawners

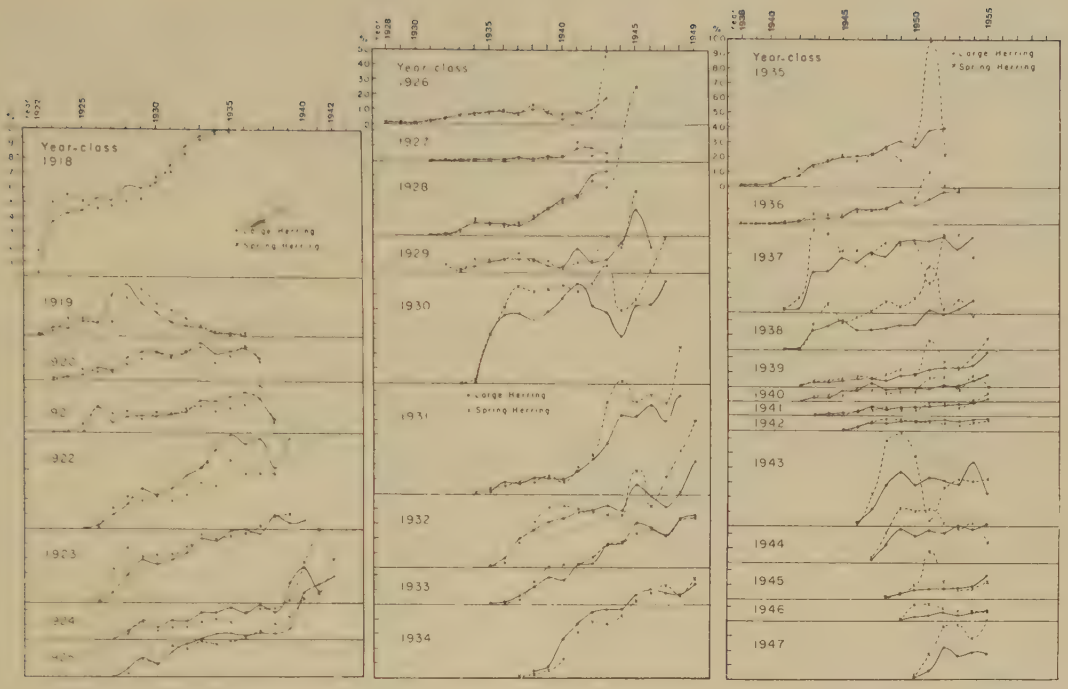


Fig. 5. Fig. 6. Fig. 7.

Figures 5–7. Percentage frequency of year-classes of Norwegian herring when younger year-classes are excluded.

show mean vertebral numbers in the proportions found in the North Icelandic herring. *In order to explain the similarity of the mean vertebral numbers of north and south Icelandic herring, it seems necessary to assume that during the period 1937—1947 a considerable part of the north Icelandic stock consisted of Icelandic summer spawners.* According to racial analysis of the south Icelandic herring during the period 1949—1955 the samples comprise 13,465 spring spawners and 11,571 summer spawners, or 46% summer spawners.

If this explanation holds true and if the samples of north Icelandic herring are representative of the stock visiting the north coast waters during these years, it must logically follow that an important part of the herring fished during the rich herring years 1937—1944 were Icelandic summer spawners.

A statistical analysis confirms the impression of the graph for the north Icelandic herring, that this stock was homogenous during a number of years.

The only alternative to my conclusion is the assumption that a selection of spring spawners with low vertebral numbers takes place and these migrate to the north coast waters. No facts, known to me, fit this explanation.

3. Norwegian waters. As previously stated no influence of the Norwegian herring can be ascertained in the S.W. Icelandic stock of herring, which has a year-class pattern of its own. Recently I suggested (Einarsson, 1954) that the reverse might be true, Icelandic herring being absorbed into the larger Norwegian stock, and it was thought that this might cause a great loss to the Icelandic area, even explain the catastrophical decline in the yield of the north coast fisheries after 1944.

Beside the marking experiments which have given interesting results (Friðriksson, 1955) there is at least one other possibility to test this hypothesis, provided the immigration of Icelandic herring into the Norwegian stock has been on a great scale. This is to test whether the Icelandic year-class pattern has any influence on the year-class pattern of the Norwegian herring. In order to examine this possibility I have calculated the relative percentage frequencies of each year-class in the older part of the Norwegian stock by excluding all younger year-classes. These calculations are graphically presented in Figures 5—7. I am greatly indebted to Mr. Finn Devold for having made the Norwegian age analyses from 1920—1955 available to me.

The test which I have made is based on the assumption that the mortality and rate of survival is the same in all year-classes. This assumption may not be unreservedly valid, as the rate of survival may decrease with increasing age. I will therefore look for some striking anomalies revealed by my test, before I venture any conclusions.

Provided this assumption is valid, it is fair to assume that a year-class retains its percentage importance when all first-time spawners have entered the spawning stock, i.e., when the herring is 6—8 years old. Until this happens the percentages should increase, due to the immigration of recruit spawners. Thus we may test by this method, if any extraneous immigrations take place or *vice versa* an emigration from the stock.

The graphs show that many year-classes follow a pattern which indicates that no appreciable immigration of extraneous origin has taken place. As typical examples of this the following year-classes can be mentioned: 1920, 1921, 1923, 1924, 1926, 1927, 1929, 1930, 1932, 1937, 1940, 1941, 1942, and 1946.

The graphs show also quite clearly the broad features in the strength of year-classes, which is usually rather uniform after the 5th year.

Next we will consider the anomalies which particularly interest us in connexion with the problem stated.

The percentage increase in the relative frequency compared with older herring, is rather conspicuous in the following year-classes: 1922, 1923, 1925, 1928, 1931, and 1933.

It may of course be argued that this rise in the relative frequency of the year-classes mentioned is due to increased mortality in older year-classes. By excluding the oldest year-classes we have limited this possibility, and on the other hand this does not answer the question why this is not experienced in all year-classes. A still more weighty argument against this is that increasing frequencies are particularly found in year-classes which we have reason to believe were strong in the Icelandic tribes of herring, e.g., 1931 and 1933. Emigration from the Norwegian stock seems probable of the 1919 and 1943 year-classes.

Significant and interesting anomalies are observed during recent years. This is most marked in 1951. In this year the 1935 year-class increased remarkably in the spring herring, and also the 1939 and 1945 year-classes. All these year-classes are known to be strong in the Icelandic herring. A striking decrease is observed in the strong Norwegian year-classes from 1937 and 1943 in the same year. This applies to the spring herring, while the large herring shows small variations. On the whole I regard the result of this test as supporting my hypothesis, and it seems reasonable to expect that immigration must have been on a rather great scale to be detectable by this rather crude method.

References

Andersson, K. A., 1956. "De stora sillfiskeperioderna på Sveriges västkust och sillen, som framkallade dem". Rep. Inst. Mar. Res., Lysekil, Ser. Biol., 5.

Devold, F., 1955. "Scandinavian herring periods". ICES 1955, Herring Committee, 69.

Einarsson, H., 1951. "Racial analysis of Icelandic herrings by means of the otoliths". Rapp. et Proc.-Verb., **128** (1): 55—74.

— 1952. "On parallelism in the year-class strength of seasonal races of Icelandic herring and its significance". Rapp. et Proc.-Verb., **131**.

— 1954. "Um uppruna og dreifingu íslenzkra fiskistofna með sérstöku tilliti til síldarinnar". Náttúrufræðingurinn, 1954, 2.

Friðriksson, Á., 1944. "Norðurlandssíldin". Rit Fiskideildar, 1944, 1.

— 1955. "Tagging of herring in Icelandic waters". Rapp. et Proc.-Verb., **140** (2): 16—18.

— & Timmermann, G., 1951. "Herring spawning grounds off the south coast of Iceland during spring 1950". J. Cons. Int. Explor. Mer, **17** (2): 172—80.

Heincke, F., 1898. "Naturgeschichte des Herings". Abh. Dtsch. SeefischVer., **2**.

Krefft, G., Schubert, K., & Sahrhage, D., 1955. "Der augenblickliche Stand der Erforschung des Nordseeherings mit besonderem Hinblick auf die Frage seiner Überfischung". Arch. Fischereiwiss., **6** (3/4).

Rasmussen, Th., 1939. "Islandssild i norske kystfarvann". Fiskeridirek. Skr., **4** (4).

Tåning, Å. V., 1944. "Experiments on meristic and other characters in fishes. I." Medd. Komm. Havunders., Ser. Fisk., **11** (3).

7.

Some Considerations Concerning the Homogeneity of the Atlanto–Scandian Herring

By O. J. Østvedt

Introduction

Several attempts have been made to subdivide the Atlanto-Scandian herring race (Broch, 1908; Johansen, 1919; Schnakenbeck, 1931; Ottestad, 1934; Runnström, 1941). The results obtained in these investigations are partly contradictory. The study of meristic characters has not given any decisive evidence for a distinction of different races. From evidence revealed by recent years' tagging experiments in Norwegian and Icelandic waters and studies of herring migration it is now generally agreed, that the Atlanto-Scandian herring is homogeneous as regards racial characters.

However, in our studies of the dynamics of the herring population it is basically important to know if components exist, which ought to be treated separately, although they cannot be distinguished by racial criteria.

Different growth types in the Atlanto-Scandian herring

Through detailed studies of herring scales Lea (1929) observed that the winter-rings of scales from young herring taken in northern Norway were sharper than the winter-rings of herring scales from the southern west coast. According to their main distributions Lea termed the two types, northern and southern respectively.

On the basis of samples of young herring ($1^1/_2$ years old) taken at the Norwegian west coast, Runnström (1936) has given further information of the geographical distribution of the two types. In northern Norway, on the Finnmark coast, 100% of the young herring have the northern scale type. In the intermediate region, between northern Norway and the Møre coast, the two types are mixed. On the south-west coast about 90% of the young herring have rings of the southern type. From this evidence Runnström concluded that the northern type of winter-rings is formed in the coastal waters of northern Norway and the southern type is formed at the south-west coast, thus sustaining Lea's theory.

In the older age-groups there is an increasing intermixing of the two types and in the spawning shoals both types are always found together. The northern type seems, however, to be predominant on the northernmost spawning grounds.

Vertebral counts of the southern and the northern type

According to Runnström (1941) the mean number of vertebrae in samples of small herring taken on the south-west coast of Norway, is significantly higher than that of herring samples taken from the north-west coast. But the mean number of vertebrae in samples of small herring (immature) with different scale types taken within the same district, did not show any significant difference.

In an attempt to check these results with the mature herring a sample of winter herring was divided according to scale type, and the mean numbers of vertebrae were calculated separately for a number of year-classes. The results for the 1934—1950 year-classes are shown in Table 1. The means tend to be slightly lower for the southern type, but the difference is significant only within the year-classes of 1938, 1943, and 1945.

It cannot be finally settled, therefore, whether the two different growth types of Norwegian herring are derived from one, geographically wide, spawning area

Table 1
Mean numbers of vertebrae of the northern and southern type of herring of the 1934-1950 year-classes

Year-class	Type	Number	Mean
1934	N	753	57·18
	S	43	·11
1935	N	545	57·22
	S	42	·21
1936	N	425	57·26
	S	36	·22
1937	N	1915	57·13
	S	53	·09
1938	N	1312	57·19
	S	80	·00*
1939	N	610	57·26
	S	100	·23
1940	N	435	57·19
	S	296	·20
1941	N	266	57·22
	S	275	·15
1942	N	154	57·14
	S	373	·12
1943	N	2837	57·13
	S	1153	·20**
1944	N	2030	57·19
	S	1699	·18
1945	N	350	57·22
	S	876	·09**
1946	N	174	57·20
	S	925	·23
1947	N	1436	57·17
	S	1548	·17
1948	N	557	57·25
	S	124	·26
1949	N	124	57·27
	S	304	·24
1950	N	1400	57·15
	S	1425	·14

* Significant difference at a probability of 0.05 to 0.02.
** Significant difference at a probability of 0 01 or less.

or from two or more distinct spawning areas. The differentiation in growth types is correlated with a geographical differentiation during the first years of life, which is due either to a different drift of the pelagic larvae from the same main spawning area, or to recruitment from geographically separated spawning grounds.

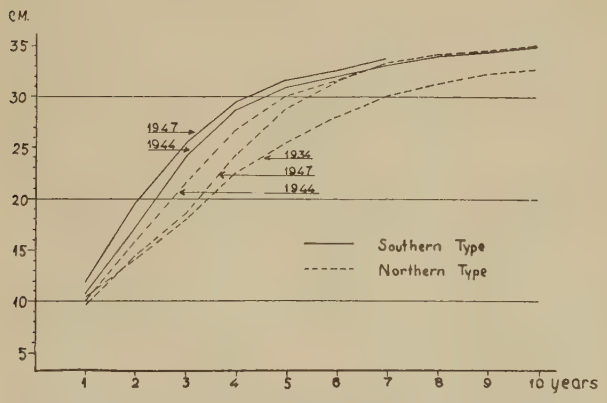


Figure 1. Age-length relationship of the northern and southern type of herring of different year-classes.

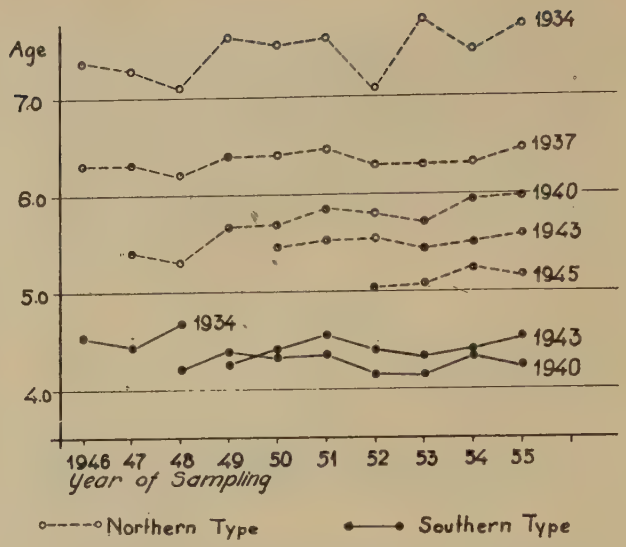


Figure 2. Mean age at first spawning of the northern and southern type of herring of various year-classes, according to year of sampling.

Growth-rate and age at first spawning

The difference in the structure of the winter-rings of the southern and the northern types is related to a different growth-rate (Runnström, 1936). Figure 1 shows the age-length relationship for the southern and the northern types of herring of different year-classes. During the first years of life the southern type has a much greater growth increment than the northern type.

The age at first spawning is closely related to the growth of the herring. The fast-growing southern type reaches maturity at a lower age than the slow-growing northern type.

The age at first spawning can be determined by means of the spawning rings on the scales. On the basis of samples of herring taken on the spawning grounds in the years 1946 to 1955 the mean age at first spawning has been calculated for each year-class and growth type according to year of sampling. The result is shown in Table 2.

It should be mentioned here that the calculated mean age at first spawning is not the true mean spawning age. The younger spawning groups of a year-class have been exposed to fishing mortalities during more fishing seasons than individuals belonging to older spawning groups, and are thus reduced in numbers compared with later incoming spawning groups. The calculated mean age at first spawning must therefore be a little too high.

Table 2
Mean age at first spawning of the northern and southern type of the 1933-1950 year-classes according to year of sampling

Northern type

Year of sampling	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950
1946	6·99	7·38	7·13	6·59	6·30	6·12	5·99	—	—	—	—	—	—	—	—	—	—	—
1947	6·60	7·28	7·03	6·66	6·30	6·20	5·85	5·42	—	—	—	—	—	—	—	—	—	—
1948	6·61	7·12	6·92	6·55	6·19	6·20	5·88	5·33	4·97	—	—	—	—	—	—	—	—	—
1949	6·88	7·63	7·36	6·73	6·39	6·28	6·19	5·68	5·21	5·16	—	—	—	—	—	—	—	—
1950	6·79	7·52	7·35	6·85	6·38	6·33	6·16	5·73	5·35	5·46	5·47	—	—	—	—	—	—	—
1951	6·40	7·63	7·65	7·11	6·45	6·32	6·32	5·86	5·44	5·29	5·53	5·06	—	—	—	—	—	—
1952	6·92	7·09	7·21	6·92	6·31	6·18	6·15	5·80	5·38	5·33	5·50	5·04	5·02	—	—	—	—	—
1953	—	7·79	7·41	6·93	6·33	6·27	6·13	5·72	5·64	5·12	5·45	4·91	5·07	5·13	—	—	—	—
1954	—	7·49	7·37	7·36	6·32	6·33	6·10	5·96	5·60	5·48	5·50	5·07	5·25	5·25	5·72	—	—	—
1955	—	7·71	7·71	7·32	6·47	6·41	6·38	6·01	5·83	5·61	5·58	5·43	5·16	—	5·79	5·92	—	—
Grand mean	6·74	7·46	7·31	6·90	6·34	6·26	6·11	5·72	5·42	5·35	5·50	5·10	5·12	5·19	5·75	—	—	—
Total number	593	2194	1261	728	4600	2844	1008	666	338	154	2765	1405	192	55	508	177	—	—
F	2·72	9·28	8·85	8·96	5·28	4·98	5·80	7·29	6·59	**1·66**	**2·17**	30·80	—	—	—	—	—	—

Southern type

Year of sampling																		
1946	4·61	4·53	4·55	4·49	4·73	4·55	4·62	4·43	4·93	—	—	—	—	—	—	—	—	—
1947	4·44	4·41	4·41	4·55	4·42	4·31	4·41	4·37	4·50	—	—	—	—	—	—	—	—	—
1948	—	—	4·38	—	—	—	4·14	4·19	4·37	4·25	—	—	—	—	—	—	—	—
1949	—	—	—	—	—	—	4·27	4·39	4·80	4·18	4·30	4·36	—	—	—	—	—	—
1950	—	—	—	—	—	—	—	4·33	4·71	4·12	4·49	4·28	4·33	—	—	—	—	—
1951	—	—	—	—	—	—	—	4·35	4·39	4·57	4·55	4·47	4·10	4·68	—	—	—	—
1952	—	—	—	—	—	—	—	4·17	4·33	4·50	4·48	4·38	4·02	4·04	4·15	—	—	—
1953	—	—	—	—	—	—	—	4·15	4·53	4·47	4·33	4·31	4·07	4·56	4·35	4·64	—	—
1954	—	—	—	—	—	—	—	4·33	4·39	4·45	4·38	4·35	4·22	4·64	4·32	4·31	4·04	—
1955	—	—	—	—	—	—	—	4·23	4·38	4·36	4·50	4·45	4·22	4·48	4·52	4·54	4·22	4·58
Grand mean	—	—	—	—	—	—	4·36	4·29	4·53	4·36	4·43	4·37	4·16	4·48	4·33	4·49	4·13	—
Total number	63	129	99	73	56	81	215	697	539	653	1673	2066	834	628	959	97	189	—
F	—	—	—	—	—	—	—	**1·34**	13·41	3·49	8·48	6·04	7·70	6·47	—	—	—	—

Heavy type = not significant heterogeneity between means for years of sampling.

When all individuals of a year-class have attained sexual maturity, it should be expected that the calculated mean age at first spawning would be constant for every year of sampling, provided that the mortality is now the same for all spawning groups of the year-class. Figure 2 shows the variations in the mean age at first spawning for some year-classes. As will be seen the mean age is not constant for any of the year-classes. An analysis of variance of the mean age at first spawning for the 1934—45 year-classes shows that significant differences exist between the mean ages of the same year-class in various years of sampling. This may be ascribed to sampling methods and mistakes in the interpretation of the spawning rings. Further it may be that our presumption of the same mortality rate for all spawning groups of a year-class (when all individuals have attained sexual maturity) does not hold true.

However, if we compare the grand mean ages for the different year-classes, shown in Figure 3, we find that for the southern type the mean age at first spawning has been nearly constant at about 4·4, over a long period of years. In contrast to this the year-classes of the northern type show a decreasing mean age at first spawning from about 7·4 for the 1934 year-class to 5·1 for the 1945 year-class. This may be ascribed to the increase in growth-rate of the northern type of herring in this period, shown in Figure 1.

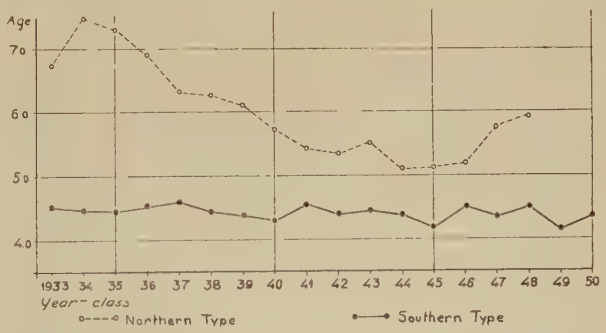


Figure 3. Average of the mean age at first spawning of the northern and southern type of herring of the 1933—1950 year-classes.

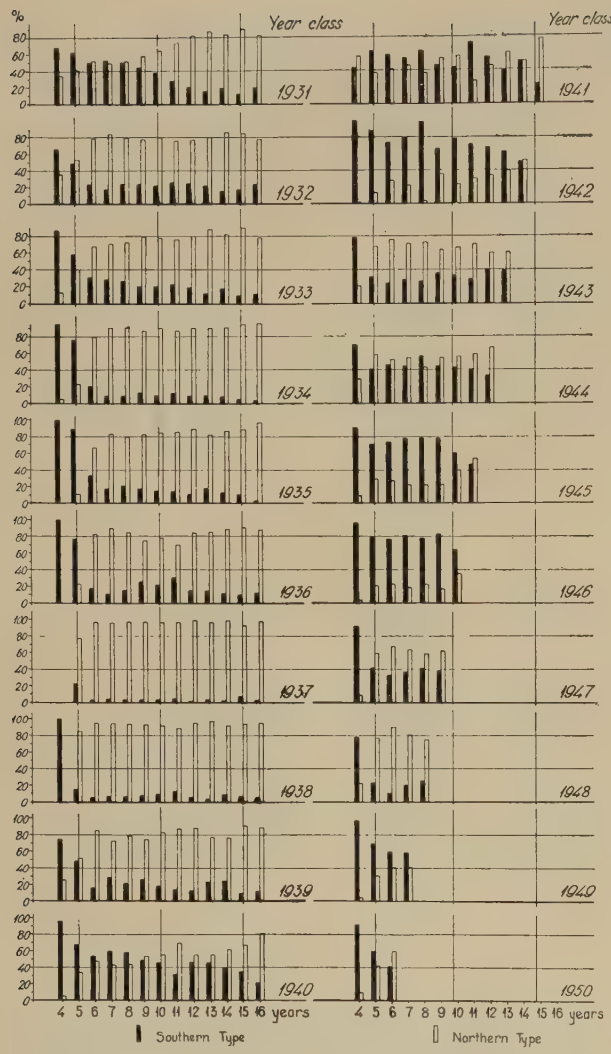


Figure 4. The ratios of the northern and southern type of herring for each year-class at different ages.

Relative abundance of the southern and the northern types

In Figure 4 the percentage ratios of the two growth types are shown for each year-class at different ages (or in different years of sampling) calculated from samples taken on the spawning grounds. The proportions of the two types show great fluctuations from one year-class to another. In the year-classes of 1931—1939, the northern type is predominant. In the year-classes born after 1940 the southern type is usually most abundant.

In each year-class the southern type dominates the first years of maturity, in accordance with the difference in age at first spawning. Owing to the small numbers of 3-year-old herring in the samples, this age-group is not included in Figure 4, but this age-group consists almost exclusively of the southern growth type.

The figure demonstrates how some year-classes are dominated by one or another of the two growth types, viz., 1937 and 1938 by the northern growth type, 1942 and probably 1945 and 1946 by the southern type. This variation in relative abundance of the two growth types seems to be related to the strength of the year-class in question. The 1934, 1937, 1943, and 1947 year-classes were especially rich (Devold, 1950, 1954). Some rich year-classes are thus mainly dependent on a strong influx of the northern type of herring. This is especially noticeable for the 1937 year-class.

According to Marty (1956) the rich year-classes have a lower growth-rate and a more northerly distribution than the poor ones. This is in accordance with our observations which show that the northern types are predominant in the rich year-classes.

Conclusion

It is evident that the northern and the southern types cannot be defined as different races. However, the existence and possible independence of these two growth types complicates our studies of the dynamics of the entire herring population.

Thus the recruitment of the two types may differ significantly from one year-class to another and the two types attain sexual maturity at different ages. It is difficult therefore, to give an early forecast of the fluctuations in abundance of the mature herring stock as long as we do not know the relative strength of the two components which are going to build up the recruit spawners each year. During the immature stages of life, the distributions of the two growth types are widely separated and at this stage they can only be treated as separate groups of young herring.

The mature part of the stock of the Atlanto-Scandian herring race is mainly subjected to exploitation. As the southern and northern type join the spawning stock at different ages they are exposed to different fishing mortalities in their early years of life. A change in the fishing intensity will therefore influence the two sub-populations differently. This may provide a means for studying the effect of fishing upon the stock.

Literature

Broch, Hj., 1908. "Norwegische Heringuntersuchungen während der Jahre 1904—1906". Bergens Mus. Årb., 1908.

Devold, F., 1950. "Norwegian herring investigations 1949". Ann. Biol., Copenhague, **6** (1949): 167—69.

— 1954. "Norwegian Sea". Ibid., **10** (1953): 147—48.

Johansen, A. C., 1919. "On the large spring spawning herrings in the North-West European waters". Medd. Komm. Havunders., Ser. Fisk., **5** (8): 1—56.

Lea, E., 1929. "The herring scale as a certificate of origin. Its applicability to race investigations". Rapp. et Proc.-Verb., **54**: 21—34.

Marty, Ju. Ju., 1956. "Fundamental periods in the life cycle of the Atlanto-Scandian herring". Trans. Knipowich Polyar. Sci. Inst., 70 pp., Moskva 1956 (in Russian).

Ottestad, P., 1934. "Statistical analysis of the Norwegian herring population". Rapp. et Proc.-Verb., **88**: 1—45.

Runnström, S., 1936. "A study of the life history and migrations of the Norwegian spring herring based on the analysis of the winter rings and summer zones of the scale". Rep. Norweg. Fish. Invest., **5** (2): 1—103.

– 1941. "Racial analysis of the herring in Norwegian waters". Ibid., **6** (7): 1—110.

Schnakenbeck, W., 1931. "Zum Rassenproblem bei den Fischen". Zeitschr. f. Morph. u. Ökologi d. Tiere, **21** (3/4).

8.

Race Formation and Marine Herring Races Biological Premises

By Ju. Ju. Marty

In considering race formation of North Atlantic herring a better understanding of the problem can be obtained by studying the corresponding features of the Pacific sub-species *Clupea harengus pallasii* which is so widely distributed in the USSR seas.

The investigations by the Soviet ichthyologists S. Averintsev (1927, 1928), A. Svetovidov (1949, 1952), A. Ambrose (1937), B. Ajushin (1947, 1951), and many others proved that the Pacific sub-species occurs in colder water than the herring of the Atlantic Ocean.

Varieties of the *pallasii* sub-species inhabit the White Sea, south-eastern Barents Sea, pre-estuarine areas of the Siberian rivers, the Bering, Okhotsk, and Japanese Seas, and the coastal waters of Alaska and Canada (Rounsefell, 1930). They spawn during the hydrographical spring, in the period when the ice is thawing, or somewhat later.

The main peculiarities of both sub-species are, from our point of view, their different reactions to water of oceanic or coastal origin. Water of oceanic origin plays an important rôle in the life of the principal races of the Atlantic sub-species (Le Gall, 1935) whereas it is the less saline coastal waters which are of great importance to the Pacific sub-species (Svetovidov, 1949).

The conditions of their ancestors may account for the different reactions of the sub-species to waters of oceanic or coastal origin.

All populations of the Atlantic and Baltic sub-species tend to prefer relatively warm waters. They usually spawn at a temperature above 5° or 6° C. This peculiarity suggests that in the period of the glaciation of Europe the Atlantic herring were distributed outside the areas affected by the suddenly changed climate. At that time the ancestors of the Atlantic sub-species seem to have existed within the borders of the continental slope somewhat southward and westward of their present habitat, i.e., in the area influenced by warm oceanic water.

The fact that many populations of the Pacific sub-species spawn at a temperature near zero, or even below zero, confirms the supposition that the ancestors of the *pallasii* sub-species were produced in the cold Polar Sea. On this assumption their need of coastal brackish water with maximum density and a temperature just above the freezing point is easily explainable. Under severe climatic conditions the physical properties of brackish waters were favourable for the species, first of all in the winter season, since the temperature in the bottom layers remained above zero.

A very marked difference in the reactions of both sub-species to waters in the Barents Sea may be observed when the herring reach sexual maturity. Young immature individuals of the Atlantic and Pacific sub-species occur both in the White Sea and in the south-eastern Barents Sea, in the same regions and under the same conditions.

The maturing individuals of the *pallasii* sub-species move to the shallow zone of the bays influenced by the discharge from land, whereas the Atlantic herring, one or two years before reaching sexual maturity, leave the eastern regions of the Barents Sea and move westward to find water of Atlantic origin.

The spawning of the populations of the Pacific sub-species takes place close to the shore at a depth of 2 or 3 metres, very often in the intertidal zone.

Frequently the sea is still covered with ice up to a distance of several kilometres off shore. Most of the Atlantic sub-species spawn at a depth of several dozens of metres in water of oceanic origin.

The Atlantic sub-species find, in water of oceanic origin, the conditions which are necessary for breeding and feeding, whereas the Pacific sub-species find these conditions in brackish coastal waters. It is here they

hibernate, breed and, not infrequently, feed. The brackish waters are of particular importance to the Pacific sub-species living in the northern part of its habitat.

The different reactions of the sub-species to coastal and oceanic water determine to a great extent the adaptability resulting in an extension of their habitats.

The adaptation to water of coastal origin leads to formation of races and their differentiation. Within the small White Sea, for instance, there are at least three populations which differ in spawning conditions and hibernation, and with relatively separated habitats (Averintsev, 1917, 1928). There are many local herring stocks in the Pacific as well, and most of them do not undertake long migrations, the herring of South Sakhalin and Hokkaido being an exception.

The adaptation to water of oceanic origin leads to an extension of the habitat as a result of migrations. During the spawning period the species are found in a relatively restricted area, while during the feeding period they travel long distances in search of food. There are no possibilities for race formation under such conditions. A most striking example of the extension of the habitat resulting from a system of migration cycles is afforded by the Atlanto-Scandian herring which in recent years have been thoroughly investigated by Norwegian and Soviet scientists (Devold, 1952, 1953; Marty, 1956). Both the passive dispersion of the young and the active migrations of the adults play a very important rôle in the life of the Atlanto-Scandian herring.

Dispersion of the young herring as a result of drift changes considerably from year to year. It is only the general direction of the drift that remains unchanged every year. The speed of the drift and the dispersion routes of the young change considerably. Therefore the greatest amount of young herring is sometimes carried into the Barents Sea by the main branch of the North Cape Current, while at other times by the coastal branch. When the drift is slow the young settle at the Murman coasts, while strong currents may carry them as far as the shallow south-eastern part of the Barents Sea.

The passive dispersion of the young does not as such lead to the formation of races since, whenever the young herring are carried by currents, they will return a year earlier or a year later to areas where the environmental conditions are favourable for reproduction. It is therefore natural that any new brood is likely to have parents which spent their first years of life under entirely different conditions.

The results of investigations on the migrations of North Atlantic cod and herring do not agree with the hypothesis of permanent migration routes. All results point to the fact that there are no "historically founded" migration routes, but a historically founded orientation exists, which first occurred in connexion with the exact conditions of a certain water basin and then became genetically fixed in the course of the long-period development of a species or a race. Every change in the distribution of water masses or currents in a basin immediately affects migration routes, because no movements or orientation of fish are conceivable beyond the exact conditions to which the fish is adapted.

Special mention should be made of the fact that the character of an adaptation and the conditions providing for the initiation of migrations or local stocks are reflected in the numerical strength of populations.

An extension of the habitat as a consequence of migrations usually results in a faster growth-rate, longer life, and greater numerical strength, whereas in most local stocks living in restricted areas a slower growth-rate and shorter span of life are noticeable and their numerical strength is considerably lower than that of migratory herring.

Classification of the Atlantic Sub-Species

When we assume that the adaptability of herring to different waters is a result of their "historical" development and adaptation of the conditions of existence present, it is justified to express our opinion regarding classification of the Atlantic sub-species. As is well known, Heincke (1898) grouped all herring inhabiting the continental shelf of the European coast into two large groups, viz., marine bank herring spawning in summer and autumn, and coastal herring spawning in spring in brackish waters near the shores. Le Gall (1935) divided herring of the continental shelf into littoral forms and brackish-water forms. The former, according to Le Gall, occur in continental waters such as the North Sea, the English Channel, and Greenland waters, while the latter live in brackish waters—the Baltic and the IJsselmeer.

By the time Le Gall wrote his paper comprehensive studies had been carried out on the Atlanto-Scandian herring (Johansen, 1927; Lea, 1929), and on the basis of these investigations he concluded that this stock was a separate race. It is the most numerous and typical race within the Atlantic sub-species. The Atlanto-Scandian herring inhabit waters of Atlantic origin and areas where these waters mix with the waters of Polar and coastal origin. These herring are to a less extent confined to coastal waters and they spawn not only off the coasts of Norway, but on the slopes of the continental shelf of the North Sea, and also along the south coast of Iceland and in the neighbourhood of the Faroes. Their spawning time coincides with the spring abundance of plankton.

In our opinion Le Gall was right in combining the Atlanto-Scandian herring and the winter/spring herring of Scotland into one group of Atlantic herring.

We presume that the summer-spawning herring of Iceland and the Faroes are quite a separate race. Their habitat is greatly influenced by warm Atlantic water. This race does not go farther to the north than 66° or 67° N. We believe that the biological isolation of this race should be beyond doubt by now. Investigations carried out by Dr. Tåning show a complete physiological separation of Icelandic summer-spawn-

ing herring and Atlanto-Scandian spring-spawning herring. Observations made by the Soviet ichthyologist LJAMIN (1956) point to an extremely high fertility of this race which is more than double that of the Atlanto-Scandian herring.

By their reaction to different waters the herring of the continental seas are clearly divided into two types, as suggested by HEINCKE, viz., marine and brackish-water herring.

The first group includes bank herring of the North Sea, English Channel, Iceland waters, and Denmark Straits spawning in regions influenced by water of Atlantic origin. As has been recorded by HEINCKE, autumn-spawning Baltic herring is very close to this type. To the second group belongs herring spawning in coastal brackish water of the North Sea and the Baltic—herring of the Firth of Forth, the IJsselmeer, the Schlei, the Limfjord, the Belts, the Dassow Lake, the Rügen, and the spring-spawning Baltic herring.

The adaptation to coastal brackish water of the latter group of the Atlantic sub-species is very similar to that of the Pacific sub-species, but there is a distinct difference in their spawning temperatures. It is characteristic that the latter group of the Atlantic sub-species seems to comprise the greatest number of local stocks, which is undoubtedly a result of its adaptation to brackish coastal waters.

Results of Investigations

The problem of different stocks within a race has never been closely studied. This problem is especially complicated as regards the Atlanto-Scandian herring.

The early investigators of the Barents Sea herring were of the opinion that several varieties of these fish differed in their habitats, growth-rate, and number of vertebrae.

Investigations carried out by the Polar Institute show that the Atlantic sub-species does not spawn in the Barents Sea, nor are there any spawning grounds in the bays of the Kola peninsula. The spawning grounds nearest to the Murman coast are those in the vicinity of the Lofotens from where the young herring are carried off by the warm waters of the North Cape Current.

The difference in growth-rates and time of first maturity of herring from different regions of the Barents Sea is due to conditions of existence and, first and foremost, to the duration of the feeding period and abundance of food in the different regions. The difference in the number of vertebrae according to regions appeared to be very slight. An interrelation was discovered between the mean number of vertebrae and the length of the young herring during their first years of life (MARTY, 1941). The same regularity was subsequently observed by Á. FRIÐRIKSSON (1944) in the case of the Icelandic herring. This dependence has not yet been explained but the very fact that herring with a slow growth-rate have a slightly higher number of vertebrae and *vice versa* warrants the assumption that the number of vertebrae cannot be a reliable criterion for distinguishing between the different stocks.

On the basis of these observations the conclusion is reached that there are no biological premises for the existence of isolated populations among the herring of the Barents Sea. The post-war investigations confirmed these conclusions and gave rise to a new problem—that of the degree of separation of the Lofoten-Barents Sea stock from the Atlanto-Scandian herring spawning in regions farther to the south.

The geographical separation of the different spawning grounds of the Atlanto-Scandian race is at present unquestionable (RUNNSTRÖM, 1934; TÅNING, 1936; FRIÐRIKSSON & TIMMERMANN, 1951; MANTEUFEL & MARTY, 1939). The spawning grounds near Iceland, at the Faroes, and along the continental slope of the North Sea lie in a great distance from each other. Nor are there continuous spawning grounds along the coasts of Norway, as great depths adjoin the Lofoten shallow waters in the south where no spawning is possible.

Certain facts suggest that the young fish of different spawning grounds are isolated. For example, young fish of Lofoten origin usually occur eastward of the Kola meridian, while most of the young which are hatched at the south-west coasts of Norway seldom occur beyond the North Cape. It is not to be doubted that all recruits spawn on the spawning grounds nearest to their feeding places. Adult herring, for example, which have already spawned several times, cover annually great distances in order to reach the region of the Polar front and may without doubt change their breeding places. It is quite probable that herring which spawned in the vicinity of Lofoten the first time, the second time may spawn in the regions of the south-west coasts of Norway.

The problem of different stocks of Atlanto-Scandian herring can only be resolved after continuous and extensive investigations into the distribution and migration of herring belonging to different, rich year-classes, and at different stages of growth and maturity.

At present we can only state that the degree of separation of herring belonging to different stocks does not remain stable throughout their life and that it decreases with age.

Herring grown up in the Barents Sea undoubtedly enter the stock of adult Atlanto-Scandian herring living in the Norwegian Sea. This recruitment can, however, not be very numerous as herring with a slow growth-rate, characteristic of the Barents Sea (L_5 not exceeding 22·5 or 23 cm.) are comparatively scarce among the adults of the Norwegian Sea. The regularity in size distribution of herring during the feeding period in the Norwegian Sea and Greenland waters is of some interest in the solution of the problem of separation of different stocks of the Atlanto-Scandian herring. Figure 1 shows the lengths of herring by regions expressed as deviations from the total range of variation for all regions. This regularity was discovered by means of mass length measurements carried out by the Polar Institute throughout a num-

Figure 1. Distribution of herring of various lengths in the Norwegian Sea and Greenland waters in July. Variation by regions are given as deviations from the total range of variation for the period from 1939 to 1956 in clusive. Total number measured 76,673 fish.

(1), northward of 77° N.; (2), between 74°30′ and 77° N.; (3), between 73°00′ and 74°30′ N., eastward of 4° E.; (4), between 71° and 73° N., eastward of 4° E.; (5), southward of 71° N., eastward of 4° E.; (6), area adjacent ot bank "600" from south-east; (7), area of bank "774" and the eastern slope of the Jan Mayen shelf; (8), western part of the Norwegian Sea between the Helgoland Ridge and the Polar front; (9), area westward of Jan Mayen; (10), Polar waters north of Iceland; (11), south-western edge of the East Icelandic Current within 64°–66° N.; (12), south-eastern edge of the East Icelandic Current.

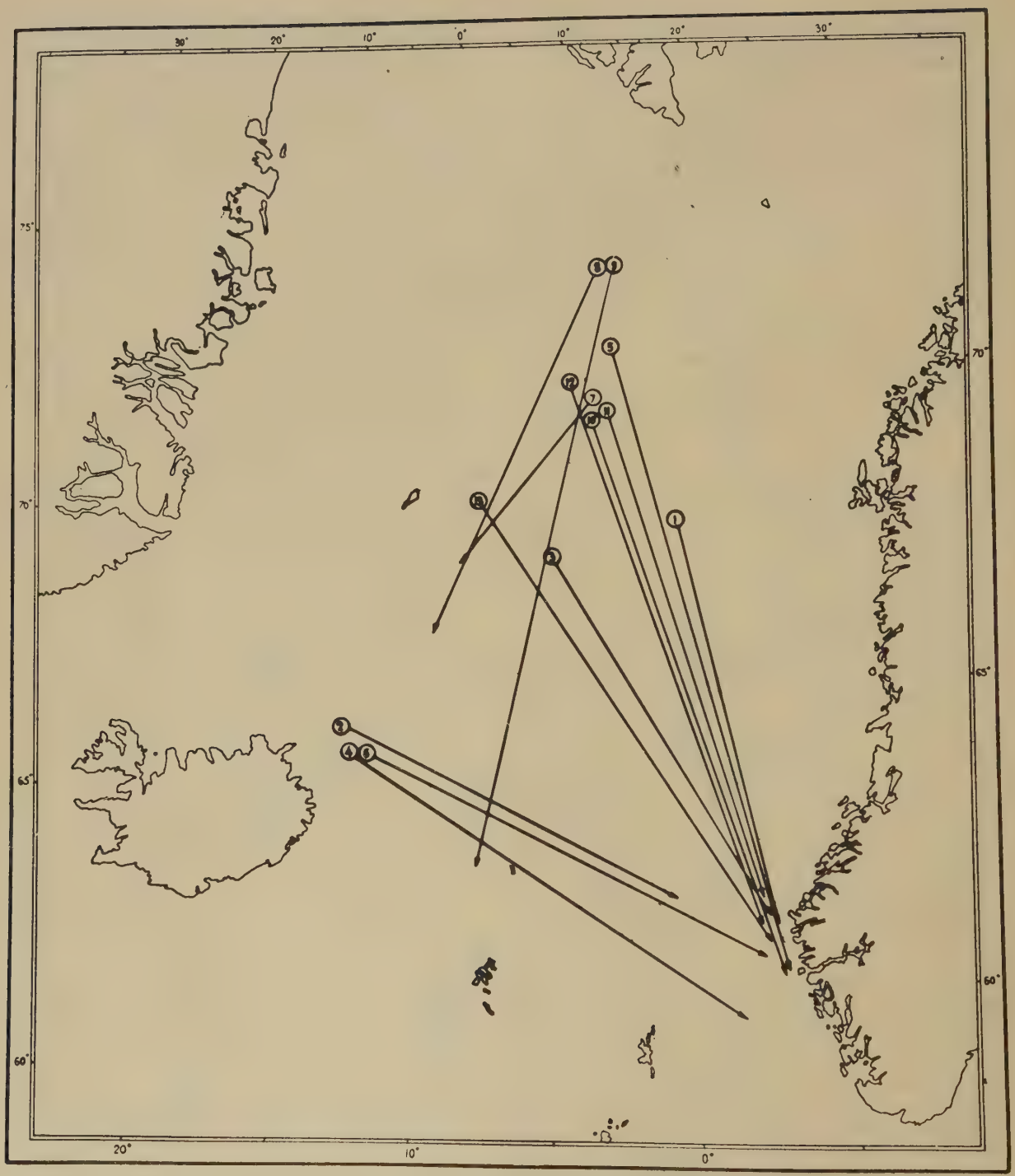


Figure 2. Routes covered by the tagged herring (see Table 1).

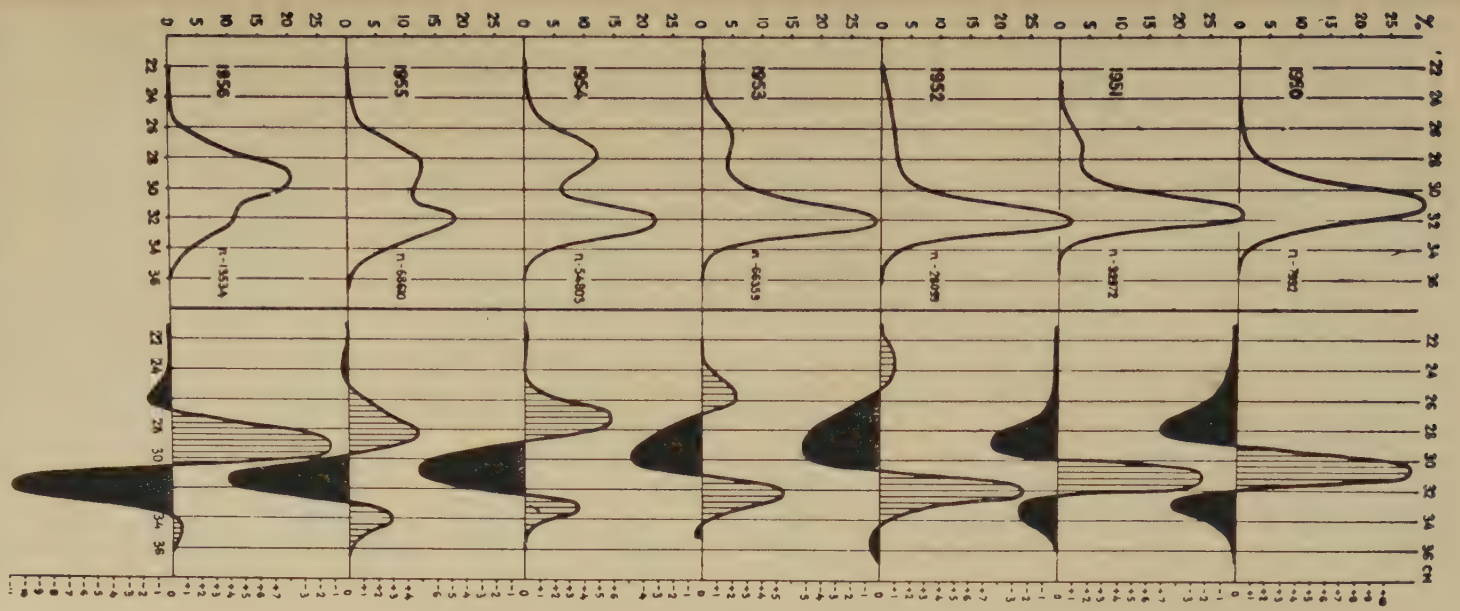


Figure 3. Size composition in the period 1950—1955. Left: ranges of variation (%). Right: deviations from the total mean range.

Table 1
Recoveries of tags

NN	Number of tag	Tagged		Returned		Days at sea	Distance covered (miles)	Average speed (miles)
		On	At	On	At			
1	4154	12/VI-1953	69°33′ N.— 5°22′ E.	31/I-1954	61°34′ N.—5°00′ E.	233	—	—
2	3544	15/VIII-1954	66°49′ N.—11°52′ W.	31/I-1955	62°55′ N.—1°55′ E.	168	240	1·4
3	4423	22/VIII-1954	69°44′ N.— 0°36′ W.	19/I-1955	62°24′ N.—6°37′ E.	150	400	2·6
4	3693	14/VIII-1954	66°24′ N.—11°31′ W.	II-1955	60°40′ N.—2°30′ E.	ca. 170	240	1·4
5	A-147	21/VII-1954	72°55′ N.— 5°06′ E.	IV-V-1955	Norway, Trondheim	253	—	—
6	3492	14/VIII-1954	66°24′ N.—11°31′ W.	IV-V-1955	at Norwegian coast	ca. 200	240	1·2
7	A-6571	3/VIII-1955	72°20′ N.— 3°38′ E.	19/IX-1955	68°55′ N.—5°30′ W.	76	270	3·5
8	A-6965	13/VIII-1955	75°00′ N.— 5°42′ E.	I/XI-1955	68°10′ N.—8°15′ W.	79	540	6·9
9	A-7025	13/VIII-1955	75°00′ N.— 5°42′ E.	16/XII-1955	64°00′ N.—8°30′ W.	125	760	6·1
10	A-6555	3/VIII-1955	72°20′ N.— 3°38′ E.	3/I-1956	62°02′ N.—4°59′ E.	154	505	3·3
11	A-6721	3/VIII-1955	72°20′ N.— 3°38′ E.	10/II-1956	62°20′ N.—5°25′ E.	191	505	2·6
12	A-7379	17/VIII-1955	63°12′ N.— 2°36′ E.	12/III-1956	62°20′ N.—5°16′ E.	208	616	3·9
13	A-7622	29/VIII-1955	70°59′ N.— 4°50′ W.	ca. 20/I-1956	62°23′ N.—5°28′ E.	ca. 140	458	3·2

ber of years in July, when all individuals of the adult stock are most remote from their spawning grounds. An abundance of large fish may be observed in the Bear Island-Spitsbergen area and in the Polar waters westward of the Jan Mayen meridian. The number of small fish increases southward along the Spitsbergen Current, while there is an increase in the number of larger fish westward of the Scandinavian Peninsula towards the Polar front.

The establishment of a general regularity in the distribution of size groups of herring throughout the Norwegian Sea and Greenland waters suggests a considerable homogeneity of the bulk of Atlanto-Scandian herring, as well as an extension of their feeding migrations with age. These suppositions have been confirmed by tagging experiments carried out by the Polar Institute in recent years. Herring tagged during their feeding period may be observed spawning off the south-west coasts of Norway and far to the north beyond the Mona Ridge, as well as in the vicinity of Jan Mayen or near the east coast of Iceland (Figure 2, Table 1).

Recoveries of tags suggest that large fish migrate from the feeding grounds to the spawning places at an average speed of about 6·5 miles per day, but the speed of younger fish does not exceed 3 or 4 miles.

Our observations on size and age composition of the adult stock of the Atlanto-Scandian herring during the feeding period point to a considerable decline in the catches of older age-groups (Figure 3). Some changes in the yield of the fishery are noted. They warrant the conclusion that the decline is not relative—which might be attributed to the abundant recruitment of the rich 1950 year-class—but absolute.

In view of these circumstances the scientists of the Polar Institute intend in the near future to intensify their investigations into the migrations of young immature fish and those which have spawned once or twice. These investigations will assist in discovering the degree of separation of the different stocks within the Atlanto-Scandian race. They will be conducted in close cooperation with the scientists of other countries—members of the ICES and, in the first place, Norway, Iceland, and Denmark.

This will require coordinated methods to be applied both on board the ships processing fish at sea, and at the herring factories of Norway and Iceland.

It is also the intention of the scientists of the Polar Institute to intensify the investigations on the drift of herring larvae and fry in different regions. These investigations will facilitate the solution of the problem of the most efficient exploitation of the rich stocks of the North Atlantic herring.

References

Averintsev, S. V., 1927. "Herrings of the White Sea". Trans. Fish. Res. Inst., **2** (1).

— 1928. "Herring of the White Sea". Ibid., **3** (4).

Ambrose, A. I., 1931. "Herring of the Gulf of Peter the Great". Proc. Pacific Inst. Mar. Fish. & Oceanogr., **6** (6).

Ajushin, B. N., 1947. "Spring herring of the north-western Okhotsk Sea". Ibid.

— 1951. "Some data on feeding herring of the northern Okhotsk Sea". Ibid., **35**.

Devold, F., 1952. "A contribution to the study of the migrations of the Atlanto-Scandian herring". Rapp. et Proc. Verb., **131**.

— 1953. "Tokter med "G. O. Sars" i Norskehavet". Fiskets Gang, 19.

Friðriksson, Á., 1944. "Norðurdlands sildin".

— & Timmermann, G., 1951. "Herring spawning grounds of the south coast of Iceland during 1950". J. du Cons., **17** (2).

Heincke, F., 1898. "Naturgeschichte des Herings". Abhandl. Deutsch. Seefischerei-Vereins, **2**.

Johansen, A., 1927. "Über die Wanderungen des Herings". Mitt. d. Dtsch. S.V., **43** (3).

Lea, E., 1929. "The oceanic stage in the life history of the Norwegian herring". J. du Cons., **4** (1).

Le Gall, J., 1935. "Le hareng (*Clupea harengus* Linné) la population de l'Atlantique Nord Est". Ann. Inst. Océanogr., N.S., **12** (1).

Lissner, H. 1934. "On races of herring". J. du Cons., **9** (3).

Ljamin, K. A. 1956. "Summer spawning herrings of Iceland and the Faeroes". Trans. Polar Inst. Mar. Fish. & Oceanogr., **9**.

Manteufel, B. P. & Marty, Ju. Ju., 1939. "Investigations on the spawning of Murman herring". Trans. Polar Inst. Mar. Fish. & Oceanogr., **4**.

Marty, Ju. Ju., 1941. "Investigations into the life cycle of Murman herring". Trans. Polar Inst. Mar. Fish. & Oceanogr., **7**.

— 1956. "Principal stages of the life cycle of the Atlanto-Scandian herrings". Ibid.

Rounsefell, G., 1930. "Contribution to the biology of the Pacific herring (*Clupea pallasi*) and the conditions of the fishery in Alaska". Bull. U.S. Bur. Fish., **45**.

Runnström, S., 1934. "The pelagic distribution of the herring larvae in the Norwegian waters". Rapp. et Proc.-Verb., **83**.

Svetovidov, A. N., 1949. "On some biological peculiarities of Pacific herring and their causes". Proc. Pacific Inst. Mar. Fish. & Oceanogr., **31**.

— 1952. "USSR Fauna. Fishes. Clupeidae". **2** (1).

Tåning, Å. V., 1936. "Herring larvae in Icelandic waters". Rapp. et Proc.-Verb., **99**.

9.

Race Characters of the Herring of the Clyde Estuary

By H. Wood

Summary

Investigation of the herring of the Clyde estuary has revealed that the stock includes both autumn and spring spawning components, but that the fishery is very largely dependent on herring of the spring spawning type, characterized by a high number of vertebrae and a low number of keeled scales (K_2).

The spring spawners have their origin on spawning grounds near the south coast of Arran and Ballentrae Bank. The progeny produced on these grounds are carried into the estuary and there they remain until the adult stage is reached, generally at the end of the third or fourth year, when as ripe or nearly ripe fish they move down the estuary to concentrate on the spawning places mentioned above. When spawning is completed the spent fish leave the estuary and adopt a more open sea existence. While some, a relatively small proportion, return to the Clyde spawning grounds in a subsequent spawning season, it is clear that the majority find new spawning places beyond the confines of the estuary.

Counts of vertebrae and keeled scales showed that autumn spawning herring of the 0-group may be on occasions quite numerous in the Firth of Clyde. There is, however, little spawning in autumn near or within the estuary and it is believed that these 0-group spawners are derived from the stock which spawns in autumn near the Isle of Man. While autumn spawners may be caught at all stages of development, this group has not been conspicuous beyond the 0-group stage.

10.

Some Remarks on Methods used in Herring "Racial" Investigations, with Special Reference to Otolith Studies

By B. B. Parrish *and* D. P. Sharman
Marine Laboratory, Aberdeen

Objectives of Racial Investigations

An essential first step in the study of the dynamics of exploited fish populations is the identification and delimitation of "unit-stocks"[1]). These may be defined as the basic biological groups into which the population can be divided for the purpose of fishery management and regulation, and which constitute "management units". The unit-stock concept has grown in importance in recent years following the development of working methods of population analysis and of their application to practical problems of fishery management and control.

The basic property of a unit-stock is that it is self-contained and its total abundance and productivity is controlled by factors acting within its boundaries. Groups possessing these properties fall into two main categories:—

(i) Geographically isolated groups which are prevented from mixing and interbreeding by migration barriers.
(ii) Reproductively isolated groups inhabiting the same general locality which mix freely during part or all of their life cycles but which do not interbreed and which possess different vital statistics.

It is clear, therefore, that different groups, which to the systematist and taxonomist may warrant different status, may possess equal status, as unit-stocks, for the fishery biologist. Only in so far as it assist him in identifying and defining unit-stocks need the fishery biologist enquire into their taxonomic status. Much of the varied terminology which has arisen in the course of "racial" investigations of species such as the herring is due to attempts to assign to the different groups, which have been identified, their true taxonomic status. Yet we are still sadly ignorant, in a number of instances, whether the so-called "races" are units in the population sense. Some standardization of terminology, for use in fishery biology, is urgently required. This can be achieved by considering the unit-stock as the basic subdivision of the population and giving equal population status to all groups satisfying this concept. The adoption of this standard would reduce the confusion of terms used in descriptive work, and would automatically define a major objective in fisheries work by designating what to the fishery biologist and fisheries administrator is a working population unit.

Methods of identifying unit-stocks

As defined above, the major task is to identify and delimit unit-stocks even though they may differ in taxonomic status. The methods which may be used in this work, in common with systematic and taxonomic work, may be grouped into (a) *direct methods*, which provide information on the movements of individuals or groups of individuals between different geographical localities and (b) *indirect methods*, which compare the characters of individuals or groups of individuals within and between different localities. The direct methods include:—

(i) Tagging or marking experiments.
(ii) Exploratory and experimental fishing surveys.
(iii) Echo-sounder surveys.
(iv) Egg and larval surveys.
(v) Studies of seasonal changes in distribution of commercial fishing operations.

Among the indirect methods are:—

(i) Comparisons of morphological characters.
(ii) Comparisons of physiological characters.
(iii) Comparisons of ecological characters.
(iv) Studies of distribution of spawning in space and time.
(v) Comparisons of fluctuations in year-class strengths between different fishing localities.

[1]) The importance and significance of the concept of "unit-stock" was discussed by Working Party 7 in the meeting of the ICNAF Research and Statistics Committee at Biarritz in March 1956.

The most difficult problems arise in the application and interpretation of the results of the indirect methods, particularly those involving comparisons of morphological and physiological characters. These difficulties stem from the variety of ways in which differences in these characters may arise: they may be the result of differences in genotype, or of differences in environmental factors operating on one genotype, or of both these effects acting together. The plasticity of these characters, under the influence of environmental factors, presents the greatest difficulties. Thus, fluctuations in temperature and other factors during the spawning and post-spawning periods may result in the values of one or more of these characters differing significantly between successive year-classes of a single unit-stock, which if not detected and recognized may lead to false subdivisions of the population. However, plasticity does not in itself invalidate the results of these methods, if interpreted correctly; it may in fact assist in the identification of unit-stocks of fish of very similar genotype but whose spawning or adolescent nursery grounds are habitually different environmentally. Clearly, for accurate interpretation of the results of these methods, knowledge is required of the nature and extent of the plasticity and of the nature of the related environmental factors. This knowledge will assist not only in the interpretation of the results obtained from these methods, but also in the choice of the most appropriate characters to use.

While both the morphological and physiological characters respond to changes in environmental factors, the nature of their responses differs in some important respects. The morphological characters, e.g., numbers of vertebrae and keeled scales are, so far as is known, fixed in early embryonic life of the individual and remain unchanged thereafter (Täning, 1944). Thus they respond to environmental factors during only a short period of time, after which their values are unaffected by environmental fluctuations. The physiological characters on the other hand, of which the rate and pattern of growth are the most important, are susceptible to environmental influences over a much longer period of time. These features provide both advantages and disadvantages concerning the use of these characters in unit-stock identification. The constancy of the morphological characters, after the initial fixation period, is clearly advantageous, but their short fixation period makes them more susceptible to the influence of sporadic short-term local fluctuations in environmental factors, which may give rise to wide variations in their values amongst the members of the same and different year-classes of a single unit-stock; equally, differences in value between members of different unit-stocks may not be detected because of temporarily similar environmental factors over their respective spawning grounds. The physiological characters are not so susceptible to short-term local fluctuations, and reflect more the average differences over longer periods between environmental factors in different areas. Again, however, they may not alone be sufficient to indicate differences between members of different unit-stocks of similar genotype, because of similarities in the growth condition of their habitats.

The choice of character to use in racial investigations, therefore, is both extremely important and difficult; no single character is likely to prove sufficient for the complete identification of the stocks of a species. Success in this work will largely depend on the detailed investigation of *several characters and methods* and on conformity of method between workers investigating different parts of the total population. Wherever possible the direct methods should be used in the place of or together with the indirect methods; only in this way can complete confidence in the interpretation of the results of the indirect methods be gained.

Methods used in herring "racial" investigations in the north-east Atlantic

Most of the European herring "racial" investigations have represented attacks on the problem of identifying unit-stocks. They have been centred on the use of the indirect methods, especially the comparison of morphological and physiological characters; only recently has the direct tagging method been successfully applied in this work.

A perusal of the vast literature on this subject in the Council's and other publications shows that not only have a large number of characters been used in this work, some of which have been discarded after fruitless preliminary trials, but different workers have concentrated their main attention on different characters.

The characters which have been used are as follows:—

A. Morphological.
   (i) Vertebral number.
   (ii) Keeled scale number.
   (iii) Fin ray number.
   (iv) Gill-raker number (a character used in recent German investigations (Krefft, 1954)).
   (v) Body proportions.
   (vi) Individual skeletal structures (for example, see contribution by J. H. S. Blaxter).

B. Physiological.
   (i) Spawning time and maturity stage.
   (ii) Growth in the first year (more precisely to the formation of the first winter scale ring: L_1).
   (iii) Growth in later years.
   (iv) The overall pattern of growth.

C. Mixed characters (characters which are morphological but which may reflect physiological differences).
   (i) Scale types.
   (ii) Otolith types.
   (iii) Overall external appearance (shape, pigmentation, etc.).

By far the greatest attention has been paid to the morphological characters, vertebral and keeled scale number, and the physiological characters, spawning time, maturity stage, and growth features. Analyses of these characters throughout the total range of distribution of herring in the north-east Atlantic has permitted a number of broad subdivisions of the total population to be made, about which there is general agreement among herring workers, and they undoubtedly provide the starting point for the delimitation of unit-stocks of herring. Thus, these investigations have demonstrated convincingly the distinction between the main body of "summer-autumn"[1]) spawning herring in the North Sea and neighbouring areas, the Atlantic "winter-spring" spawning group (spawning season February—May); and the local populations of "winter-spring" spawning herring in the North Sea, Transition Area, and the Baltic.

Analyses of these characters have been less successful, however, in determining the unit-stocks of herring *within* each of these main groups, about which there is much less agreement among herring workers, and which are the focus of attention in herring racial studies at the present time.

A further deficiency of these characters is the difficulty in determining accurately the extent of the overlap in space and time of members of these three major groups, knowledge of which is of importance in dynamical studies. This stems from their relatively small range of statistical variation (especially the morphological characters), the large degree of overlap of values, even between the most widely separated groups, and the plasticity of the characters within any one group. These features create difficulties in the dissection of samples of values taken from a region of mixing of groups. Maturity observations taken along with measurements of these characters assist in this dissection, particularly in some seasons, but they are of no use by themselves to distinguish individuals of different groups during the adolescent stages of the different groups, or in periods of the year when the maturity stages of the adult members of the different groups are the same. Clearly, for this important task, characters by which *individual fish* can be identified, rather than those requiring statistical manipulation of large samples, are to be preferred.

Use of "individual" characters

"Individual" characters which have been studied by some workers but which hitherto have not been adopted extensively in European herring investigations, are scale and otolith types. The use of these characters in racial work depends on the recognition of phenotypic and/or genotypic differences in the structure and disposition of growth zones and rings, which reflect differences in the growth pattern, metabolism, and morphology of fish. Extensive studies of scale characters have been made on herring in the Norwegian area by Lea (1929), while otolith types have been studied recently by Einarsson (1951) in Iceland. Lea was able to show, from a study of the pattern and nature of growth zones and winter-rings on the scales of herring off Norway, the presence of groups of scales showing different distributions of growth zones and differences in the nature of the winter-rings. He was able to detect on the scales without measurement, therefore, differences between the overall growth pattern in different groups of individuals and the reflection of differences in the conditions in which these groups lived. On the basis of these results Lea strongly advocated a widespread international survey of scale types of herring, in the spawning condition throughout the European area, as a means for determining the independence of different spawning groups. Hodgson (1934, 1950) also demonstrates the value of this character in southern North Sea herring studies.

Einarsson's major observation was that the structure and appearance of the nucleus of the otolith provided evidence of the time of hatching of the fish so that, from a study of this character, individuals from mixed samples of any maturity stage could be assigned to one or other of two major spawning groups, the "summer-autumn" and "winter-spring" groups in the Icelandic area. This important work undoubtedly constitutes one of the most significant recent steps in herring racial studies.

In his published work, Einarsson describes only the differences in the structure and appearance of the otolith nucleus between the major herring groups in the Icelandic area: he makes no reference to differences in other otolith features, comparable with those identified on the scales by Lea in his earlier studies. If such features are also present, then the value of the otolith as a racial character may be even greater, and it may be used not only for distinguishing between groups of herring hatched at different times but also in the identification of groups having the same spawning season, but different growth characteristics and general biology.

In recent years a study has been made, at the Aberdeen Laboratory, of the features of otoliths from herring caught in the northern North Sea in order to assess their value as "racial" characters in this area.

Otolith studies in the northern North Sea

Since 1952 large numbers of otoliths have been studied from fish captured in the Scottish drift-net fisheries in the northern North Sea. The major aims of this work have been:—

(i) To establish the general validity in northern North Sea studies of Einarsson's method of identifying individuals hatched in different seasons from the nucleus characteristics.

[1]) This term is used here to describe the body of herring which spawns in the North Sea between August and December or January, on grounds ranging between the Scottish east coast and the eastern entrance to the English Channel, and which has been termed "Banks" herring, or "Banks" and "Downs" herring by many herring workers.

(ii) To examine the otolith for features other than nucleus type, so as to establish the presence of distinct "otolith types" amongst each major spawning group.

Most of this work has been carried out by low power examination of the otoliths with reflected light against a black background, but recently a large-scale photographic examination has been made to facilitate the identification of particular otolith features. The photographic method is described in the Appendix to this report. This programme of work is still in progress and, as yet, only otoliths from herring sampled in the northern North Sea have been studied extensively. It is not yet possible therefore to report in detail on the results of the second of the above aims but only to draw attention to some preliminary observations of differences between otolith characteristics in herring fished in the Scottish area.

Validity of nucleus characteristics

The first step in establishing the general validity of the nucleus characteristics in the North Sea herring groups was to determine the range of variation in these characteristics amongst herring from a wide range of localities and times, and relate these to other measurable "racial" characters such as length, maturity stage, vertebral number, and L_1.

As in the Icelandic investigations, two main types of otolith have been identified; those with a clear hyaline nucleus, and those with an opaque or almost opaque nucleus. Examples of these two main types are given in Plates 1 and 2. Again, as in the Icelandic material, considerable variation has been found amongst these two types; the size of the hyaline centre varies amongst individuals of the same age and maturity stage of the first type, and the opacity varies amongst individuals of the second type. Thus, the same range of nucleus types, as identified by Einarsson, is observed in the North Sea material and difficulties arise in assigning some otoliths to their spawning group on the basis of the nucleus characteristics alone. However, a study of the general characteristics of the otoliths (e.g., general texture and appearance, size of growth zones, and "winter" zone structure) of the two main "nucleus" types has shown that other differences can also be detected between them, and these can be used along with the nucleus characteristics to identify the two main types and so assist in the discrimination between otoliths having doubtful nucleus characteristics. The nature of these differences are described in a later section.

Analysis of these two main otolith types from a wide range of times and localities in relation to the state of maturity, length, and vertebral number has shown, as in Einarsson's investigations, that the otolith type having a hyaline nucleus can be identified with a "summer-autumn" spawning group of herring, and those having the opaque nucleus with a "winter-spring" spawning group. The following main results have been obtained:—

(i) Herring in maturity stages VI and VII, caught in the north-eastern North Sea and to the north and west of the Shetlands in the period March—May, possess otoliths of the "opaque" nucleus type.

(ii) Herring of maturity stages VI and VII on the spawning grounds off the Scottish east coast in August and September have otoliths of the "hyaline" nucleus type.

(iii) Herring of maturity stages IV—VII on the Fladen and Gut grounds in September and October belong to the "hyaline" nucleus type.

(iv) Herring with the "opaque" type nucleus, in all maturity stages, have high mean vertebral counts, corresponding with those of one or more of the well-known "winter-spring" spawning groups in the European area; and those categorized as "hyaline" type have lower mean vertebral counts corresponding with the well-known North Sea Bank herring.

(v) The mean lengths of herring of the "opaque" type are generally greater than those of the "hyaline" type, particularly amongst the older age-groups. This is again in keeping with the observed differences in growth-rate between the well-known "winter-spring" and "summer-autumn" spawning groups of herring.

(vi) The L_1s of the herring with the "opaque" type are smaller on average than those of the "hyaline" type.

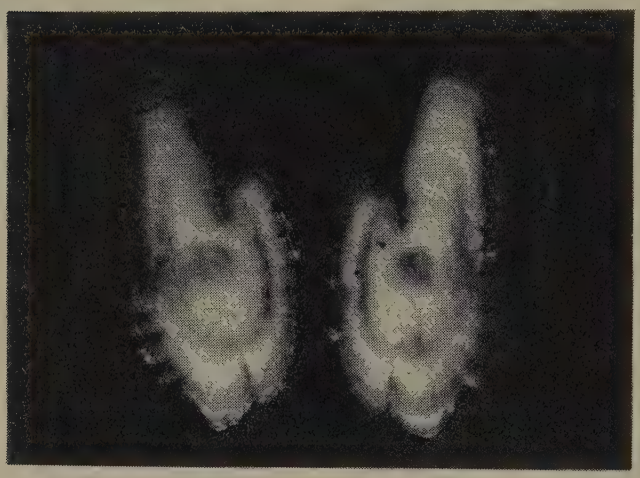
An example of the breakdown into otolith types of samples taken from the northern North Sea, and the maturities, mean lengths, and vertebral numbers of each is given in Table 1. Summarized here are the results of the analysis of samples taken in July and August 1953, from the fishing grounds to the east and south of the Shetlands; these are well known as a region of mixing of feeding and pre-spawning shoals of the main North Sea "summer-autumn" spawning group and of "winter-spring" spawners from the North Sea and other areas.

These data show that none of the characters other than otolith type is sufficient to allow an accurate subdivision of mixed samples of those groups to be made, particularly of the younger age-groups, in which a large proportion of both spawning groups are in maturity stage I; their lengths are approximately the same, and the distributions of vertebral number show a large overlap of values so that the total distribution cannot be accurately split into the two components. Values of L_1, calculated from scale samples, are also inadequate by themselves for this purpose again because of the large overlap of values of the two types.

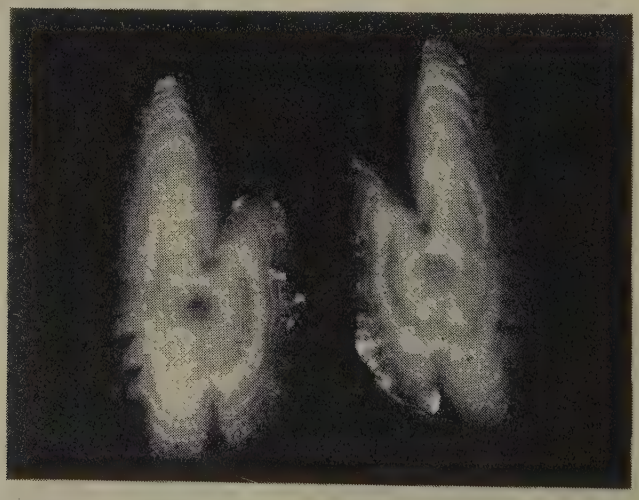
Thus, it is evident that the nucleus characteristics, along with other general features of the otoliths described below, (a) provide a satisfactory method for identifying and distinguishing between the members of the two main spawning groups inhabiting the northern North Sea, which constitute distinct biological groups between which the exchange of spawners

PLATE I.

OTOLITHS FROM 'SUMMER-AUTUMN' SPAWNING HERRING



A). A PAIR OF OTOLITHS SHOWING 3 WINTER ZONES AND A HYALINE CENTRAL NUCLEUS.

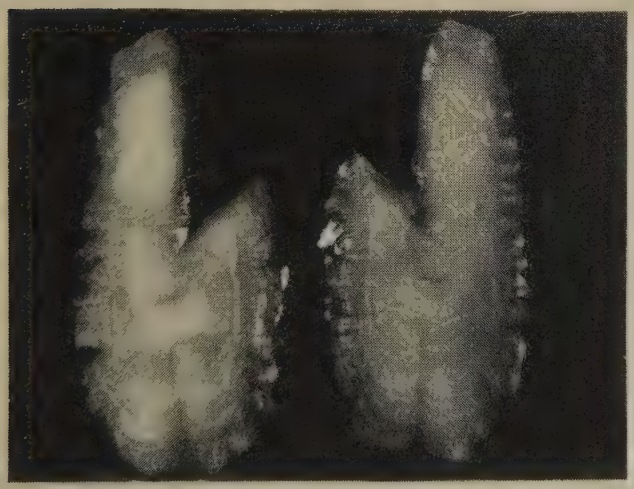


B). A PAIR OFOTOLITHS SHOWING 8 WINTER ZONES.

PLATE 2.

OTOLITHS FROM 'WINTER-SPRING' SPAWNING HERRING.

A). A PAIR OF OTOLITHS SHOWING 3 WINTER ZONES WITH AN OPAQUE CENTRE.



B). A PAIR OF OTOLITHS SHOWING 7 WINTER ZONES.

Table 1. Otolith types in Shetland samples in July and August 1953

Age (winter-rings)	Otoliths of "hyaline" type						Otoliths of "opaque" type						% of Otoliths not categorized
	Mean length (cm.)	Mean VS	Maturity state (%) I	II & VII-II	III & IV	V-VII	Mean length (cm.)	Mean VS	Maturity state (%) I	II & VII-II	III & IV	V-VII	
2	25·1	56·55	64·0	18·0	18·0	—	25·4	57·05	97·2	2·8	—	—	8·7
3	27·4	56·57	10·8	30·6	56·8	1·8	28·6	56·95	42·6	56·8	0·6	—	7·4
4	28·3	56·46	4·3	42·8	50·0	2·9	30·2	57·02	9·1	87·2	3·7	—	6·1
5	28·3	56·68	2·8	59·1	33·7	4·4	29·8	57·20	7·7	65·2	27·1	—	10·2

is negligible or absent, and (b) are more efficient for this purpose than the conventional "racial" characters used hitherto. The two groups which they identify are the main North Sea "summer-autumn" spawning body of herring which spawn between August and December or January on grounds between the Scottish east coast in the north and the Southern Bight in the south, and the "winter-spring" spawners which spawn between February and May on grounds ranging from the Norwegian coast and the continental shelf to the European coastal areas and the English Channel.

Other otolith features

Although the nucleus characteristics provide a satisfactory means for identifying the majority of individuals belonging to the two major spawning groups of herring in the North Sea and neighbouring areas, they are not sufficient by themselves for studying the possible subdivision of each of these groups into separate unit-stocks. They do not, for example, provide a satisfactory means by themselves for determining the relations between the northern and southern members of the North Sea "summer-autumn" spawning group, or between groups of "winter-spring" spawners from different areas which mix in the North Sea during the feeding season.

A detailed study of large samples of otoliths from different localities, including herring nursery areas, has shown, however, that significant differences can be recognized between other otolith features, which assist, not only in the initial identification of the two main spawning groups, but which also reflect differences in the physiology and growth of herring living in different habitats during adolescent life. The features of greatest significance are:—

(i) The general texture, shape, and size of the entire otolith.
(ii) The size and distribution of the growth zones.
(iii) The appearance of the "hyaline" winter-rings.

Differences among these features which have been recognized between the two main spawning groups are as follows:—

(i) Otoliths of most members of the "winter-spring" spawning group have a "finer" texture and possess a "smoother" outline than the "summer-autumn" spawners.
(ii) The first growth zone is generally smaller amongst members of the "winter-spring" spawning group than amongst the "summer-autumn" spawners.
(iii) The "winter" zones are usually different in general appearance between members of the two groups.
(iv) The relative dimensions of different parts of the otolith differ on average between the two groups. The antirostrum of the winter-spring spawners is larger, relative to the size of the rostrum, than in the summer-autumn spawners, which presents an easily recognized, overall difference in general shape.

These features provide useful additional criteria for the initial identification of members of the two main spawning groups. It is likely that most of these features, like the nucleus characteristics, are phenotypic and reflect differences in general physiology and growth of herring inhabiting different nursery grounds during their adolescent phase. It is significant in this respect that the differences between some of these features in the two groups (e.g., the appearance, texture, and size of the otoliths and the nature of the "winter" zones) are less marked in the older age-groups, for which there is generally greater difficulty in identifying individuals of the two groups.

Marked differences between these otolith features have also been recognized within each of the main spawning groups, and it has been possible to identify distinct otolith types which appear to correspond with further subdivision of these groups.

Otolith types amongst "winter-spring" opaque nucleus group

Two main otolith types have been recognized so far amongst the "winter-spring" spawning group sampled in the northern North Sea. Examples of these are shown in Plate 3, A and B. Members of these two types cannot be distinguished by their nucleus characteristics, but they reveal marked differences in a number of other features; in particular they show differences in overall shape, texture, and size, and in the distribution of the growth zones and the nature of the "winter" zones.

The features which characterize the two types are as follows:—

PLATE 3

EXAMPLES OF TYPES OF OTOLITHS FROM 'WINTER-SPRING' SPAWNING HERRING

A) FROM SHETLAND FISHERY. WITH FIVE CHARACTERISTIC WELL DEFINED WINTER ZONES.

B) FROM SHETLAND FISHERY. WITH FIVE WINTER ZONES.

PLATE 4

EXAMPLES OF TYPES OF OTOLITHS FROM 'SUMMER-AUTUMN' SPAWNING HERRING

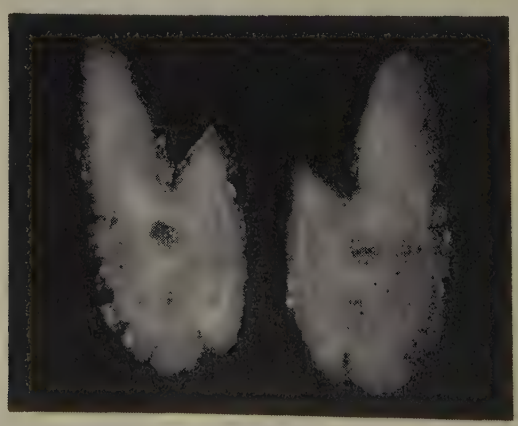
TYPE A

FROM MORAY FIRTH NURSERY GROUNDS. THIN SHARP FIRST WINTER ZONE

TYPE B

FROM BLØDEN FISHERY. WIDE FIRST WINTER ZONE

TYPE C

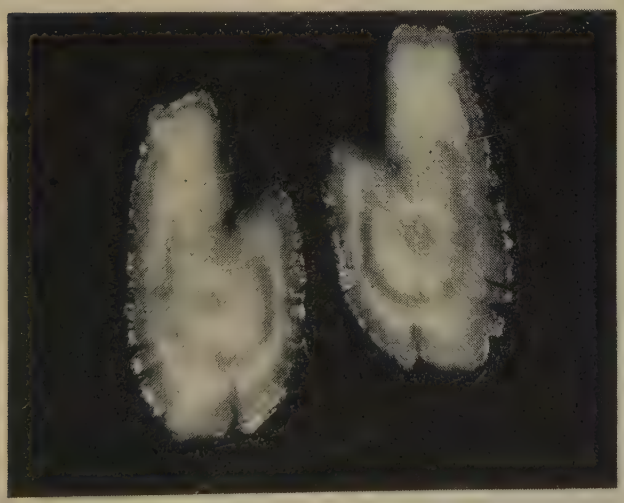


FROM BUCHAN FISHERY. THIN SHARP FIRST WINTER ZONE, SIMILAR TO TYPE A

PLATE 5

EXAMPLES OF TYPES OF OTOLITHS FROM 'SUMMER-AUTUMN' SPAWNING HERRING

TYPE D. FROM BUCHAN FISHERY. THIN SHARP FIRST WINTER ZONE; LARGE FIRST GROWTH ZONE.



TYPE E. FROM BUCHAN FISHERY. WIDE FIRST WINTER ZONE.

Type A: (i) Smaller otoliths with fine texture and relatively smooth outline.
(ii) Characteristically "hard", sharp winter zones.
(iii) Relatively small first, second, and third growth zones, followed by larger fourth or fifth growth zones.
(iv) Relatively large antirostrum.

Type B: (i) Relatively large otoliths with relatively rough texture and deeper sulci than type A.
(ii) Characteristically "soft" or diffuse first and second "winter" zones.
(iii) Relatively large second growth zone, followed usually by progressively smaller growth zones in later years.
(iv) Relatively small antirostrum.

These two types of otolith can be easily distinguished amongst mixed samples, and type A can usually be picked out by naked eye examination of the otoliths.

These otolith types appear together in samples taken from a number of localities in the northern North Sea. Both of them have been located in the summer drift-net fishery to the east of the Shetlands, in the spring fishery, in the north-eastern North Sea, in April and May, on the Fladen grounds in September and October and to the north and west of the Shetlands in March and April. Type B otoliths are the ones most commonly represented amongst spawners on the North Minch spawning grounds in February—April, and they are found also amongst Clyde spawners. Type A on the other hand, has appeared only occasionally in these areas.

As yet, the origin and identity of these two herring types have not been established conclusively, but evidence at our disposal indicates that at least type A belongs to the Atlanto-Scandian group. Otoliths of this type have been identified in a small sample of otoliths, kindly supplied by Mr. Finn Devold from the Norwegian spring herring fishery, and the scales of the North Sea herring of this type are of the characteristic "northern" type identified by Lea (1929). It is significant in this connexion that this otolith type was the most prominent one amongst samples of spawning herring taken off the north-west coast of Shetland in March and April 1953.

Type B otoliths have been identified amongst a wide range of age-groups (2 to 8 years) in the northern North Sea drift-net catches, but type A has not been identified in herring less than five years of age (4 "winter" zones). It is probable, therefore, that the nursery grounds of herring of type A are located in areas remote from the northern North Sea, and that they are feeding immigrants to this area. It appears, on the other hand, that herring of type B have their nursery grounds in or in the vicinity of the northern North Sea. The general characteristics of this type are similar to the "southern" Norwegian scale type identified by Lea, but the relation between them cannot as yet be firmly established.

The racial characters other than otolith and scale type, of these two types are very similar. Both types appear in the Scottish summer drift-net fisheries mostly in maturity stages I—III, their total length distributions are similar, although those of type A are usually rather smaller age for age than those of type B and their mean vertebral counts, ranging between 57·10 to 57·30, are not significantly different. Identification and separation of these two groups could not therefore be made from these characters alone or in combination.

The analyses so far carried out have been confined almost entirely to herring caught in the northern North Sea and the Minch, so that they constitute no more than a first step in the possible use of otolith characters in the identification of unit-stocks within the "winter-spring" spawning group. The next important step is extensive sampling on the major spawning and nusery grounds of this group in the European area in order to see whether further otolith types exist and, if so, whether their interrelations can be determined.

Otolith types amongst "summer-autumn" hyaline nucleus group

Unlike the "winter-spring" spawning group, which has a relatively restricted spawning season between February and April, the "summer-autumn" spawning group in the North Sea and neighbouring areas has a prolonged spawning season which extends from August in the north to December or January in the south. The possible subdivision of this major group into distinct northern and southern components, which mix freely during the feeding season, but which segregate into separate spawning communities, has been the subject of intensive study for many years; today it constitutes one of the most important problems in European herring biological studies.

Although no such distinct otolith types have been identified amongst members of this group as in the "winter-spring" spawning group, a number of important features have been recognized which undoubtedly reflect major differences in the physiology and growth of groups of individuals during adolescent life, and which may be of value in determining the extent of mixing of individuals derived from different parts of the total spawning area. The features which are most prominent are:—

(i) the width and sharpness of the first "winter" zone, and
(ii) the size of the first-year growth zone.

When the otoliths from herring of the "summer-autumn" group, sampled at widely scattered localities in the northern North Sea, are categorized on the basis of these features, the majority fall into two main groups. These are:—

(i) Otoliths with a wide or diffuse first "winter" zone and a relatively small first growth zone. These are illustrated in Plates 4B and 5E.

(ii) Otoliths with a thin, sharp, well defined first "winter" zone and a wide range in size of the first growth zone. These are illustrated in Plates 4A, 4C, and 5D.

The significance of these features in the study of the intermixing of groups of "summer-autumn" spawners in the North Sea is evident from the study of the distribution of these features in otoliths taken, (a) from different nursery areas in the North Sea, (b) from different age-groups and maturity stages of adult herring in the northern North Sea.

The following results are of particular significance:—

(i) Otoliths obtained from "halflin" herring in the nursery areas of the upper Moray Firth and Firth of Forth fall mainly into the "thin first-winter zone" category and have relatively small first growth zones (Plate 4A). This otolith type has characterized the members of three consecutive year-classes in this area.

(ii) Otoliths from a sample, kindly provided by Dr. BERTELSEN, of two-year-old herring from the Bløden fishing grounds in the south-eastern North Sea were mainly of the "wide first-winter zone" type and possessed relatively small first growth zones (Plate 4B). Unfortunately only one sample has been analysed from this area, so that it is not possible to assess the constancy of this feature at the present time.[1])

(iii) Both of the above types of otoliths have been identified amongst the recruit age-group (2 "winter" zones) in the Buchan and Shetland summer fishery (Plates 4C and 5E). The type illustrated in Plate 5D has not been identified so far amongst either the Scottish or the Bløden ground nursery area samples.[1])

(iv) Observations on the relative proportions of these two otolith types show an increase in the proportion of the "wide first-zone" type with age, both amongst the feeding and spawning concentrations in the Scottish area.

(v) Both types of which the wide-ringed type was the more abundant, have been observed amongst small samples of otoliths from the East Anglian fishing area and kindly supplied by Mr. RICHARDSON of the Lowestoft Laboratory.

As yet, insufficient sampling of otoliths over the total range of distribution of the "summer-autumn" spawning group in the North Sea, especially of the adolescent and spawning concentrations, has been carried out for a full interpretation of these observations to be made. They are sufficiently striking, however, to warrant an intensive study of the otolith features of adolescent and spawning herring of this major spawning group throughout the North Sea and adjacent areas. It is considered that this may provide valuable information on the exchange of herring between the northern and southern North Sea (and perhaps elsewhere) and on the location of the main nursery areas for each of the major spawning grounds.

[1]) Since this report was written further samples of otoliths from the Bløden area have been examined by kind permission of Mr. POPP MADSEN, and specimens of the type shown in Plate 5D have been observed in these samples.

Origin of nucleus and other characteristics

At present it is not possible to gauge to what extent any of the differences between the otolith characteristics discussed above are genotypic, but it is likely that most of them are phenotypic and reflect differences in growth and metabolic activity during the early stages of development of herring hatched in different seasons and localities.

The nucleus characteristics which have been observed can be explained as follows, in terms of the well-known periodicity in otolith structure between different seasons:— Investigations of zone formation in herring otoliths by LISSNER (1925), and in this laboratory, show that hyaline zones are formed in adolescent herring mostly during the "winter" period October to April, while opaque zones are laid down in the "summer" months May to September. If this periodicity also applies during the period of formation and initial growth of the otolith, then otoliths of herring hatched in late summer and autumn (between September and December or January) will be laid down mostly in "winter" conditions and will be hyaline, while those hatched in winter and spring (between February and April) will be formed and grow mostly in "summer" conditions and will be opaque. On this general basis, also, the size of the hyaline nucleus of herring hatched in the "summer-autumn" period will be determined by the amount of otolith growth during the period of "winter" conditions. Little is known of this at the present time, but it is probably related to the growth in length of the herring. Therefore, it is to be expected that on average, the *size* of the hyaline nucleus will be greater in otoliths of herring hatched in summer (August and September) than in those hatched later in the season (November and December). However, this trend in nucleus size between early and late hatched individuals is likely to be masked by variations in growth-rate amongst individuals hatched at the same time and different times in different localities, and in variability amongst individuals in the dates at which hyaline zone formation commences and ceases. The size of the hyaline nucleus is not likely therefore to be a very sensitive index of the time of hatching of individual herring, but it is likely to give a general indication of whether samples are composed mainly of herring hatched either early or late in the "summer-autumn" period.

As well as showing variation in the size of the hyaline nucleus, the otoliths of both the "summer-autumn" and the "winter-spring" groups exhibit variation in the size of first opaque growth zone. This feature, like the nucleus size is probably also related to the total growth of the herring up to time

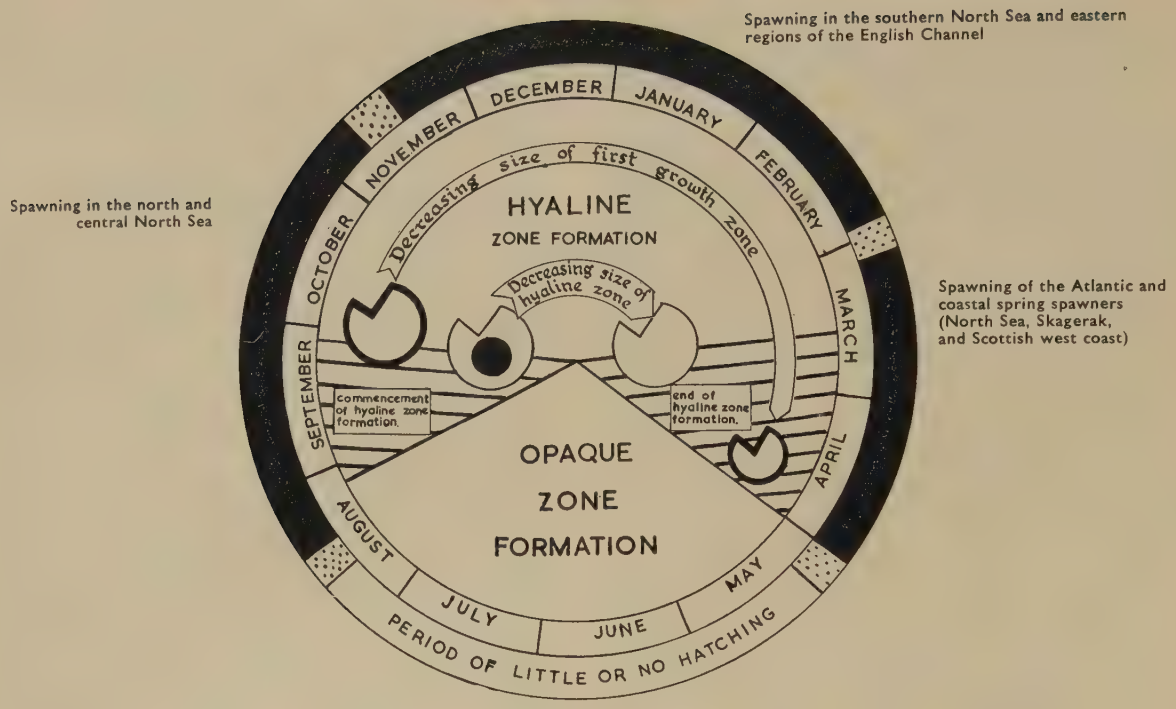


Figure 1.

of formation of the first winter zone. Thus, as with the hyaline nucleus, it is to be expected that the size of this opaque zone will be greater on average amongst members of the "summer-autumn" group than amongst the "winter-spring" group. Again, however, this trend will be masked by variations in growth-rate between individuals hatched at the same time but occupying different nursery grounds, and so will reduce the value of this feature alone as an individual index of origin. It does provide, however, important additional information to use along with the nucleus characteristics in assigning individuals to one or other of the major spawning groups, and to determine whether samples of the "summer-autumn" group are composed principally of early or late hatched fish.

The expected relationship between time of hatching, nucleus characteristics, and size of the first growth zone are represented schematically in Figure 1, which also shows the months in which hatching and initial otolith formation and growth takes place in herring derived from different spawning areas in the North Sea and adjacent regions.

It is evident from this diagram that, while the otolith characteristics of the main body of "summer-autumn" spawned fish, hatched between August and November exhibit marked differences from those hatched in the "winter-spring" period March and April, some overlap of otolith characteristics is to be expected between herring derived from different spawning areas and seasons. This is most marked and presents the greatest problems in identification of individuals amongst herring derived from the spawning concentrations in the Southern Bight of the North Sea and the eastern regions of the English Channel, in the period November to February. A detailed study of otoliths from spawning fish in this area is required in order to gauge the total range of variation of otolith characteristics amongst them and to determine the differences throughout the spawning season and with age.

The differences between the other otolith features which have been identified in these investigations, and particularly the nature of the "winter" zone, are probably the result of differences in the environmental complex over the nursery grounds in different areas. From their associations with types of scale rings described by Lea, it seems probable that the "thin-sharp" zone is characteristic of a relatively cold winter habitat in which metabolism and growth are severely restricted, while the "wide-soft" zone is characteristic of a warmer winter habitat.

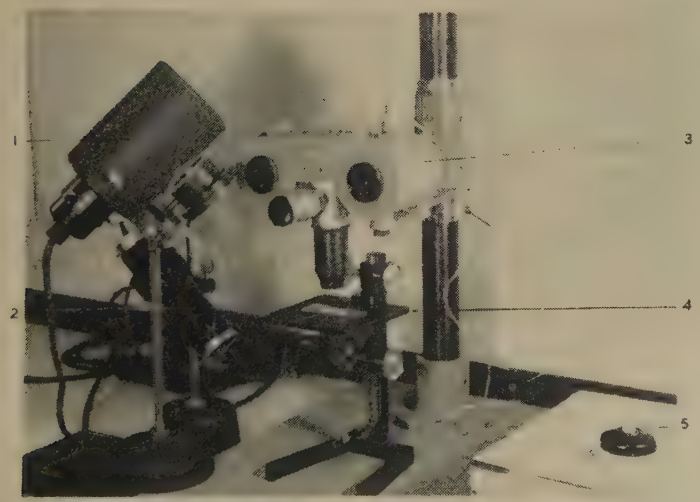
Conclusions

From the results obtained so far in the investigations of otolith characteristics of herring in the North Sea the following conclusions may be drawn concerning their value as an individual character in unit-stock identification.

(i) Members of the two main spawning groups, "summer-autumn" and "winter-spring" which

PLATE 6.

A) OTOLITHS MOUNTED FOR PHOTOGRAPHY.



B) PHOTOGRAPHIC APPARATUS. 1. LAMP FOR REFLECTED LIGHT. 2. LAMP FOR TRANSMITTED LIGHT. 3. CAMERA. 4. VERTICALLY MOVING STAGE FOR FOCUSING. 5. SWITCH FOR SHUTTER OPERATION.

mix in the northern North Sea during the non-spawning period can be identified individually with sufficient accuracy for quantitative evaluation of their respective abundance in the fisheries.

(ii) Members of these two major groups constitute distinct biological units between which interbreeding is usually considered to be, and probably is negligible or absent. For all that, a small number of herring with otoliths having "summer-autumn" characters have been recorded in spawning condition in spring in the Firth of Forth and North Minch areas, but no herring spawning in the "summer-autumn" period, August and September, in the northern North Sea have been observed with distinct and definite "winter-spring" otoliths.

(iii) Differences in one or more features of the otoliths of herring within each of these main groups, which probably reflect major differences between the conditions in the nursery areas, provide a possible basis for studying the inter-mixing and movements of individuals from the nursery areas to the spawning grounds, and between different spawning grounds with age. This may be of particular value in studying the interrelations between herring spawning in the northern and southern North Sea, and in delimiting the principal nursery grounds for each spawning centre.

References

Einarsson, H., 1951. "Racial analyses of Icelandic herrings by means of the otoliths". Rapp. et Proc.-Verb., **128** (1): 55—74.

Hodgson, W. C., 1934. "The natural history of the herring of the southern North Sea". Buckland Lectures for 1933.

— 1950. Ann. Biol., Copenhague, **6**: 175—77.

Krefft, G., 1954. "Untersuchungen zur Rassenfrage beim Hering". Mitt. Inst. Seefisch., **6**: 12—22.

Lea, E., 1929. "The herring's scale as a certificate of origin. Its applicability to race investigations". Rapp. et Proc.-Verb., **54**: 21—34.

Lissner, H., 1925. "Die Altersbestimmung beim Hering mit Hilfe der Otolithen". Ber. Dtsch. Komm. Meeresforsch., N.F., **1**: 181—98.

Lucas, C. E., 1956. Chairman's report of Working Party 7 of meeting of Research and Statistics Committee I.C.N.A.F.

Tåning, Å. V., 1944. "Experiments on meristic and other characters in fishes". Medd. Komm. Havunders., Ser. Fisk., **11** (3): 1—66.

Appendix

A Method of Photographing Herring Otoliths

1. Mounting the otoliths

The procedure is as follows:— a white fibre washer 1 cm. in diameter is placed on a standard glass slide 3×1 inches ($2{\cdot}5 \times 7{\cdot}6$ cm.). The particulars of the otolith are marked in Indian ink on the washer. A drop of Canada balsam is placed in the centre of the washer and in it the otolith is then positioned (having previously been cleared in xylene for approximately thirty seconds). Mounting is completed with a cover glass (Plate 6A).

2. Photography

Perhaps the most difficult problem to overcome in photographing otoliths is to obtain an even illumination. Photography with reflected light only gives disappointing results, due to a "falling off" of the more transparent edge of the otolith. This method, however, is satisfactory when otoliths are visually examined through a microscope. To overcome the poor definition of the otolith edge, transmitted polarized light is used in conjunction with reflected light. To polarize the light, one polaroid is placed behind the camera lens and one in the condenser mouting, which is rotated to obtain a plane of extinction. This type of illumination gives the otolith a sharply defined outline with a dark background. The more central part of the otolith is illuminated by reflected light. To reduce shadows the lamp is used with the beam as near vertical as possible.

The photographs are taken with a 35 mm. Shackman autocamera which can expose 200 negatives inch square ($2{\cdot}54$ cm. square) on 20 feet of film. The camera is fitted with a 35 mm. f2 Cooke speed panchro lens which is attached to an extension tube giving approximately $\times 3$ magnification. There is also a reflex eyepiece fitted to the extension tube which allows each otolith to be focused separately. The shutter and film transport are operated electrically (Plate 6B).

11.

The Composition of the Minch Herring Stocks

By I. G. Baxter

Introduction

Herring fishing is in progress in the Minch almost continuously throughout the year. There are, however, two main periods of high activity and these occur between November and March and between June and September. A fairly reliable picture of the distribution of herring concentrations in the Minch can be gained from an examination of the fishing grounds (Figs. 1 and 2). The main fishing grounds throughout the year are basically the same, they lie along the east coast of the Outer Hebrides from the Butt of Lewis to Barra Head and generally within the 50 fathom contour. Between June and August, however, the grounds in the North Minch extend from the Lewis to the mainland coast and during that period of the year the catches are composed of maturing autumn spawners together with a mixture of immature adolescents of spring and autumn origin. Between September and May, the grounds along the east coast of the Hebrides are fished for spent and recovering spent autumn spawners but the catches also contain varying proportions of maturing spring spawners and adolescents of both groups.

During February and March there is generally a fishery for spawning herring along the north-west mainland coast; and although this fishery is of short duration, very large catches of spring spawning fish are sometimes obtained. Other fishing grounds of less importance are located around the north-west coast of Skye and off the islands of Canna and Coll. These grounds are fished mainly between the autumn and early summer for recovering spents and adolescents of both races.

In the Minch herring are caught by drift-net and ring-net. The landings from the North Minch, which is more open and exposed, are obtained almost

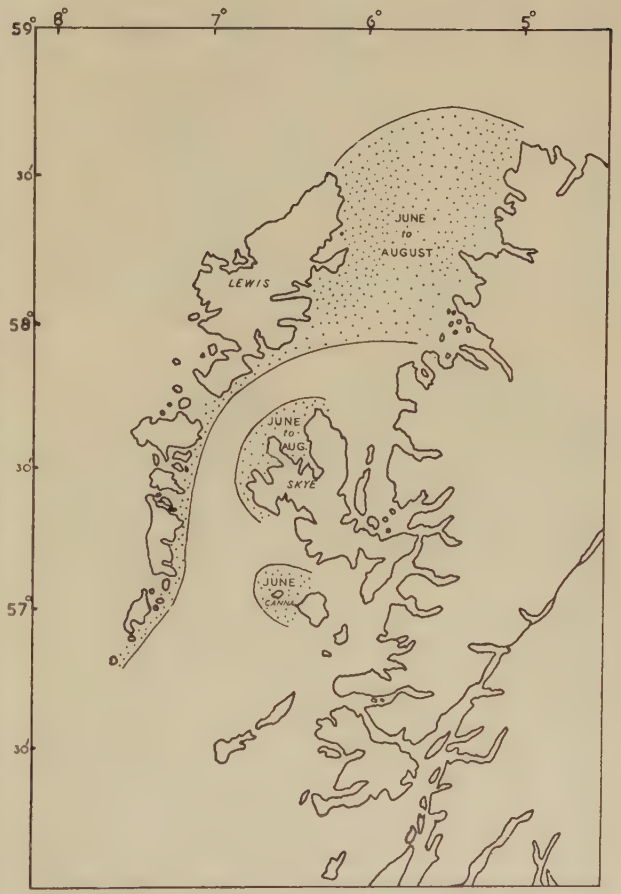


Figure 1. Herring fishing grounds in the Minch between June and August.

Figure 2. Herring fishing grounds in the Minch between September and May.

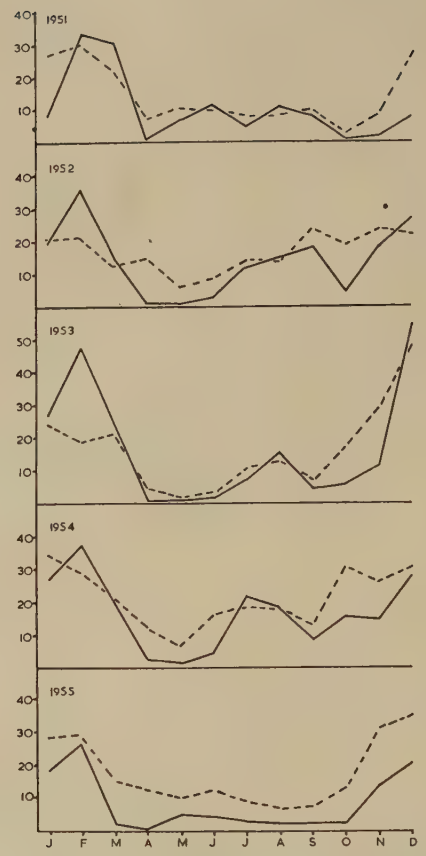


Figure 3. Minch herring landings by drift-net. January—December 1951—55.
——— = total landings (1,000 crans)
------ = average landings per arrival (crans)

entirely by drift-net, while in the South Minch where the coast provides more shelter fishing is carried out by ring-net as well as drift-net vessels.

Since most of the fishing vessels are not based locally the exploitation of the Minch stocks is somewhat erratic and depends to a large extent on the productivity of other herring fisheries nearer the home bases. From Figures 3 and 4 in which total landings and landing per arrival for drift-net and ring-net vessels are given, it will be seen that the late autumn and winter fisheries are generally more productive than the summer fishery.

Earlier work on the herring in the Minch has been of a limited nature and has been concerned mainly with the composition and characters of the spring spawning shoals along the north-west mainland coast. References are found in the publications of Johansen (1919), Wood (1923—37), Bowman (1923), Storrow (1923—40), Schnakenbeck (1927), Lissner (1934), and Le Gall (1935).

The aims of this paper are, firstly, to describe the characters of the spring and autumn herring populations in the Minch and, secondly, to discuss the affinities of each group to neighbouring stocks of spring and autumn spawners.

The material has been obtained to a large extent from samples of commercial catches of both drift-net and ring-net vessels between 1951 and 1955. Some of the data on spawning grounds have been collected during the cruises of the F.R.S. "Clupea" over the same period.

Problems affecting the study of a mixed population

The herring stocks in the Minch are composed of spring and autumn spawners. Representatives of each group occur in varying proportions in the majority of Minch catches throughout the year. It is essential, therefore, when studying the characters of each group to have some reliable method of separating them. Although the degree of maturity may be used with success to discriminate between the adults of the two groups during the spawning periods, it is not a reliable

method to use at other periods of the year and certainly never in the case of adolescent herring.

Other biometric characters commonly used in defining herring stocks such as vertebral numbers, keeled scales, l_1 material etc., have a limited value when dealing with a mixed population. These characters can only be used to define the population as a whole, and not in discriminating between individual groups within it. Einarsson (1951), faced with similar problems while studying the herring populations in Icelandic waters, found that herring otoliths could be used in discriminating between the spring and summer spawning groups in Icelandic waters. He showed that the otoliths of the majority of Norwegian spring spawners were characterized by having opaque nuclei, while the otoliths of the Icelandic summer spawners had clear or hyaline nuclei. The technique and validity of the otolith method for discriminating between different groups of herring in Scottish waters is discussed in another paper contributed to this symposium (Parrish and Sharman). The description of the characters of each Minch group, which follows, is based to a large extent on the initial analysis of the material into spring and autumn spawners by otoliths.

A. The Minch Spring Spawners

1. Spawning grounds

The main centres of spring spawning in the Minch have been known for some time. Bowman (1923) demonstrated that they were situated off the north mainland coast between Cape Wrath and the Island of Handa. Wood (1930) confirmed these observations by showing that most of the herring taken on the mainland grounds during the spring fishery were in a spawning condition.

Spawning appears to take place along the mainland coast from Cape Wrath to Gairloch but particularly in the vicinity of the Islands of Handa and Bulgie (Fig. 5). The distribution of the fishing fleet suggests that spawning occurs almost entirely within the 40 fathom contour. Early records reveal that this fishery for spawning herring was a regular feature and that very dense shoals were usually encountered. More recently, however, it has been less successful and indeed the fishery failed completely in 1952 and 1955. During these two years the landings of spawning herring were almost entirely limited to small localized catches obtained by fishermen using anchored drift-nets close inshore.

Table 1, in which the maturities of samples, from different areas in the Minch are given, shows that the composition of the herring shoals on the mainland grounds was quite different from those occurring on other fishing grounds in the Minch during February and March. The mainland grounds therefore must be considered as the spawning grounds during this period.

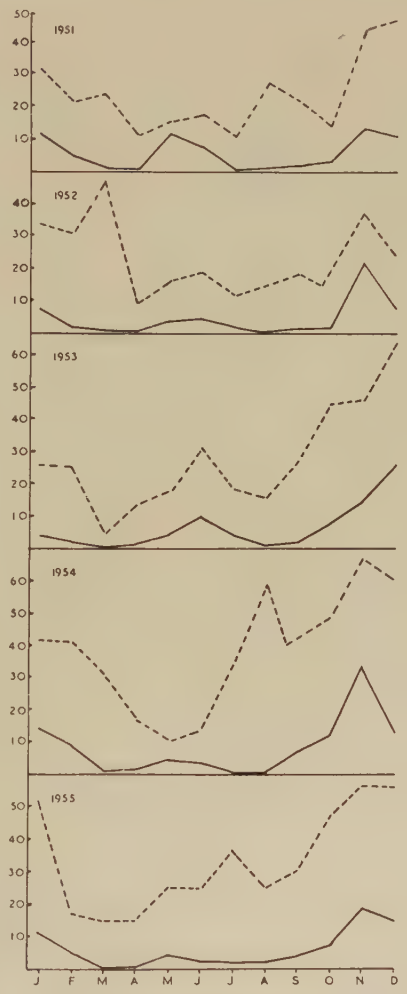


Figure 4. Minch herring landings by ring-net January—December 1951—55.
——— = total landings (1,000 crans)
------ = average landings per arrival (crans)

2. Race characters of the Minch spring spawners

(a) *Vertebral number.*

The Minch spring spawners appear to be similar to other spring spawning concentrations in Scottish waters. Wood (1936) found that the mean vertebral count (one sample) was 57·07, while for Shetland spring spawners he obtained values ranging between 57·01 and 57·08. In the Clyde he found that there was some variation from year to year in the mean

Table 1
Percentage maturities of samples from the Minch in February and March 1951-55

February

	Year	Stage								No. of fish
		I	II	III	IV	V	VI	VII	VII-II	
Mainland Grounds	1954	0·7	1·2	17·1	17·6	18·0	**44·8**	0·2	0·5	433
Lewis Grounds	1952	15·6	16·4	2·4	2·7	5·5	0	7·8	**49·6**	255
	1953	5·2	9·0	9·2	19·8	18·6	1·8	—	**36·4**	500
	1954	28·9	8·1	0·8	0	1·2	15·5	7·3	**38·2**	250
	1955	2·8	1·6	13·0	17·2	5·2	2·8	5·3	**52·0**	500
Harris N. & S. Uist Grounds	1952	20·0	8·9	0	0·4	0·7	0·4	22·2	**47·4**	270
	1953	3·6	11·7	9·7	4·0	0·4	0·4	0·8	**69·4**	250
	1954	32·8	9·6	0·4	0·8	0·4	0	0·8	**55·2**	250
Barra Grounds	1951	2·9	6·6	0·8	0·4	0	0	0·5	**88·8**	214
	1955	0	3·6	8·8	13·2	1·2	2·0	6·8	**64·4**	250

March

	Year	Stage								No. of fish
		I	II	III	IV	V	VI	VII	VII-II	
Mainland Grounds	1951	0	0	1·0	7·7	8·7	**70·8**	6·7	5·2	496
	1954	0	0	0	1·9	3·8	**92·5**	1·9	0	53
	1955	0	0	0·82	—	—	**98·37**	—	0·82	245
Lewis Grounds	1952	5·5	8·9	0·7	2·7	2·3	0·2	10·0	**69·7**	439
	1953	5·0	28·1	0·4	0·8	0	1·0	7·8	**56·9**	498
	1954	13·2	24·6	0·6	0·2	0	1·2	1·4	**58·8**	500
	1955	3·7	3·7	2·9	7·7	2·0	3·1	3·1	**73·7**	350
Barra Grounds	1951	2·5	4·5	0·4	1·6	0·4	0	5·6	**84·0**	214
	1952	3·6	14·9	0·6	0	0	0	7·7	**73·4**	222
	1954	16·8	22·0	0	0·4	0	0·8	0	**60·0**	250
	1955	11·2	5·6	0·4	0·4	0	0	12·4	**70·0**	250

Table 3
Percentage vertebral distribution of Minch spring spawners of individual year-classes on the spawning grounds (Feb.-March)

	1951				1954		1955	
Year-class	1948	1947	1946	1945	1951	1953	1952	1951
VS Age...	3	4	5	6	3	4	3	4
59	—	1·09	—	0·60	—	—	—	—
58	18·75	17·39	11·76	16·17	16·37	14·09	15·26	19·44
57	62·75	59·78	67·65	57·49	70·76	70·47	69·47	63·89
56	18·75	20·11	20·58	25·15	16·37	15·44	14·74	13·89
55	—	1·63	—	0·60	—	—	0·53	2·78
Number of fish	16	184	34	167	171	149	190	36
Mean	57·00	56·96	56·91	56·91	57·04	56·99	56·99	57·00

Figure 5. Spring and autumn spawning grounds in the Minch.

//// = spring spawning grounds
:::: = autumn spawning grounds

vertebral number, the values given ranged between 57·03 and 57·21. Other workers gave means of 56·78 (Schnakenbeck, 1927) and 57·13 (Le Gall, 1935) for the Minch spring spawners. Schnakenbeck's figure, however, was based on a single sample of 58 fish. Prior to 1939 an important trawl fishery for herring was carried out between July and October on the Klondyke grounds, which lie between Barra Head and the north coast of Ireland, and Le Gall (1935) gives the mean vertebral count of these herring as 56·97. Heincke (1898) gives a mean of 56·97 for spring spawners off Barra Head, where a fishery for large fat recovering spring spents used to take place (prior to 1939) in the early summer months.

The distribution and vertebral means obtained between 1951 and 1955 on the spring spawning grounds are shown in Table 2; they are in fairly close agreement with earlier records from this area. The amount of variation one can expect between year-classes is indicated in Table 3 where the distribution

Table 2
Percentage vertebral distribution of Minch spring spawners on the spawning grounds

	All age-groups			
VS	Wood (1936)	1951 (March)	1954 (Feb.-March)	1955 (March)
59	0·6	0·73	0·23	—
58	21·3	16·38	15·14	16·88
57	63·8	59·41	72·25	68·35
56	13·2	22·49	12·39	13·92
55	1·2	0·98	—	0·84
Number of fish	159	409	436	237
Mean	57·07	56·93	57·03	57·01

of vertebrae and means for individual year-classes are given. The vertebral means range from 56·91 for the 1945 year-class to 57·04 for the 1951 year-class.

(b) *Length at formation of first winter-ring* (l_1).

The l_1 values for the main age-groups on the spring spawning grounds between 1951—55 are given in Table 4. Although the range extended from 7—18 cm., the largest number of observations lay between 11 and 15 cm., the mode occurring at 13 cm.

On the whole the Minch values are fairly uniform, suggesting that a single homogeneous stock is involved. They may be compared with the distribution of l_1 lengths of spring spawners in Shetland waters in 1953 and 1954 (Table 5, Parrish) which shows a greater variation between year-groups and means. It must be remembered, however, that we are not dealing with a single spawning concentration off Shetland, as is confirmed by the analysis of the otolith material from spring herring at Shetland. From the large number of growth calculations made by Lea (1910), it is seen that the mean l_1 values of the Norwegian spring spawning herring ranged from 7·0 cm. in northern Norway to 9·3 cm. in southern Norway, while he gives mean l_1 value of 11·9 cm. for spring spawning herring at Shetland. Storrow (1923—40), working on the stocks of herring found in the winter fisheries around the coast of Britain between 1923 and 1940, obtained mean l_1 values for Minch spring spawners ranging from 10·0 cm. in 1927 to 11·1 cm. in 1935. These values are 2—3 cm. lower than those obtained in the Minch during the period 1951—55, but are higher than the values obtained by Lea for Norwegian spring spawners.

3. Growth

Perhaps one of the most remarkable features of the Minch spring spawners is their fast growth-rate during the first three years of their life. By the time the first winter-ring has been laid down, the majority have reached 13—14 cm. in length. These fish first begin to appear in the commercial catches, as herring with one winter-ring on their scales, during the summer and autumn, when some have attained a length between

Table 4
l_1 distribution of Minch spring spawners on the spawning grounds

1951

Age cm....	8	9	10	11	12	13	14	15	16	17	18	Total	Mean
3	—	—	—	2	3	3	2	2	—	—	—	12	12·92
4	—	1	4	16	30	**33**	27	21	10	—	—	142	13·15
5	—	1	2	6	4	5	4	1	1	1	—	25	12·48
6	—	1	4	13	22	**38**	34	14	5	4	1	136	13·25
7	—	—	—	—	2	2	1	2	—	—	—	7	13·43

1954

Age cm....	8	9	10	11	12	13	14	15	16	17	18	Total	Mean
3	—	—	1	13	37	**79**	62	33	6	2	—	233	13·38
4	—	2	4	20	26	**48**	25	13	3	—	—	141	12·82

1955

Age cm....	8	9	10	11	12	13	14	15	16	17	Total	Mean
3	—	5	7	13	36	**41**	39	17	6	—	164	12·93
4	—	1	1	8	8	6	—	1	1	—	26	12·04

Table 5
l_1 distribution of Shetland spring spawners[1])

May-August 1953

Rings cm....	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Total	Mean
2	—	—	—	1	6	**22**	19	19	17	5	2	1	—	—	92	12·48
3	—	—	3	5	32	37	**40**	**40**	26	12	1	—	1	—	197	12·05
4	—	1	2	4	5	8	17	22	**37**	6	2	1	—	—	105	12·80
5	1	1	1	8	4	8	3	4	3	2	1	—	1	—	37	11·23
6	—	2	6	10	9	4	9	7	6	1	1	1	—	—	56	11·02
7 + ...	—	—	8	**25**	16	12	9	**19**	10	10	5	—	—	—	114	11·46

May-August 1954

Rings cm....	6	7	8	9	10	11	12	13	14	15	16	17	18	Total	Mean
2	—	—	—	—	—	4	5	7	10	4	—	2	—	32	13·41
3	—	—	1	5	12	37	**53**	50	33	12	2	1	—	206	12·41
4	—	—	1	9	22	35	**41**	32	16	5	1	—	—	162	11·83
5	—	—	—	1	2	2	8	**23**	22	8	4	—	1	71	13·46
6	1	3	4	3	7	6	5	4	1	2	—	—	—	36	10·50

[1]) From PARRISH, personal communication.

Table 6 A
Mean lengths of adolescent spring spawners

	Rings	Mean length cm.	Number of fish
North Minch 1955 (October-December)	1	23·01	280
South Minch 1955 Coll Bank (December)...	1	23·94	155

Table 6 B
Mean lengths of Minch spring spawners on the spawning grounds at point of age

Age	3	4	5	6	7
1951.....	27·64 (25)	29·22 (195)	29·63 (43)	30·15 (220)	30·45 (11)
1954.....	28·29 (257)	29·61 (153)	30·00 (15)	—	—
1955.....	27·68 (190)	29·28 (36)	30·73 (11)	—	—

Table 7
Age composition (%) of Minch spring spawners on the spawning grounds (Feb.-March)

Year	Age...	3	4	5	6	7	8	9	Number of fish
1951		3·62	41·63	8·37	44·12	2·26	—	—	442
1954		50·43	43·02	4·27	0·57	0·57	0·57	0·57	351
1955		69·57	27·05	2·42	0·97	—	—	—	207

Table 8
Age composition (%) of Minch spring spawners

June-December

Year	Rings...	1	2	3	4	5	6	7	8	9	Number of fish
1953		12·55	38·38	33·95	2·95	3·32	3·32	3·32	1·11	1·11	271
1954		3·59	70·70	19·12	4·76	0·67	0·33	0·08	0·17	0·50	1,198
1955		49·93	14·65	28·45	3·41	3·27	0·28	—	—	—	703

Table 9
Maturities of spring spawners (%)

June-August 1954

Rings	Stage...	I	II	III	IV	V	VI	VII	VII-II
2		84·75	14·53	0	0·24	—	—	—	0·48
3		29·6	47·2	6·4	0·8	2·4	—	—	13·6
4		13·89	38·89	5·56	—	—	—	—	41·67

23 and 24 cm. The mean lengths of 1-ringed spring spawners taken in North and South Minch catches in 1955 are given in Table 6A and the mean lengths of 3—7 years old spring spawning herring on the spawning grounds are shown in Table 6B.

The main body of the fish which spawn as three-year-olds have reached a mean length of between 27 and 28 cm. Estimations of growth after the third year are regarded as biased, since the majority of the herring will have spawned as three-year-olds and migrated out of the Minch. The four- and five-year-old groups will contain a percentage of slower growing individuals which are spawning for the first time.

4. Age composition

The most striking feature revealed by the age-composition data from the spring spawning grounds given in Table 7 is that the stock during this period was composed of relatively young fish. Herring older than 6 years formed less than 3% of the total. In 1951 six years old herring of the 1945 brood predominated. This year-class was also outstanding in the Icelandic spring spawning stock but not in the Norwegian spring herring at Iceland (Fridriksson, 1953). During 1954 and 1955, however, over 90% of the stock on the spawning grounds were composed of 3- and 4-year-old herring.

Table 8 shows that the age composition of spring spawning fish in the Minch between June and December was very similar to that obtained on the spawning grounds during the following February and March (Table 7). This suggests that the herring on the spawning grounds are recruited in the main from the adolescent stock located in the Minch during the pre-spawning period. Wood (1951) found similar conditions in the Clyde.

The maturities of the Minch spring spawners between June and August 1954 given in Table 9 show that, although the majority of the Minch spring spawners appear to spawn for the first time as three-year-olds, a percentage do not spawn until they are 4 or 5 years old. It would appear, therefore, that after spawning for the first time the majority of spring spawners leave the Minch and do not return even to spawn.

Discussion

Johansen considered that the spring spawning herring of Norway, Faroes, and Iceland could be grouped into one race which he termed the "Atlanto-Scandian" spring herring. Norwegian and Icelandic tagging experiments have shown how closely related these stocks of herring are. Lissner (1934) thought that the spring spawning herring of Scottish waters should also be included in Johansen's Atlanto-Scandian group. Le Gall (1935) proposed that all the spring spawning herring of the North Atlantic should be grouped together under the title "Harengs

Atlantiques". The important characters of these herring were as follows:—

1. A mean vertebral number of 57 or more,
2. A relatively fast growth-rate, and
3. A spawning period during the early months of the year.

Le Gall subdivided this main community into two sub-groups.

(a) *The "Atlanto-Scandian" group* as defined by Johansen.

The group is characterized by having a mean vertebral number greater than 57. In this group he included the spring spawning herring of Norway, Iceland, Faroes, Shetland, Viking Bank, White Sea, and Murmansk coast.

(b) *The "Hiberno-Calédoniens" group.*

This group is characterized by having a mean vertebral number close to 57. In this group Le Gall included the spring spawning herring of the Minch, the Klondyke grounds, and the Celtic Sea.

Le Gall believed that these two groups were separated geographically in the open Atlantic, the *Atlanto-Scandian group* being distributed to the north of the Wyville Thomson Ridge and the *Hiberno-Calédoniens group* to the south.

It has been shown (see above) that, after spawning for the first time, the majority of the spring spawners migrate out of the Minch and do not return even to spawn. The site of their spawning grounds in later years is a matter for conjecture but it seems possible that they might form part of the shoals of herring which are believed to spawn along the continental shelf off the west coast of Scotland and Ireland. It is not unreasonable to believe that the spring herring of the Clyde and Celtic Sea also contribute to this group which spawns along the continental shelf.

The physical conditions under which the *Atlanto-Scandian* and Minch spring spawners spawn are quite different. The *Atlanto-Scandian group*, of which the Norwegian spring spawners are the main component, spawn in conditions of relatively low temperature (5—6° C.) and salinity $33‰$—$34‰$ (Runnström, 1941 b), in contrast to the Minch spring spawners, in temperatures of $> 7°$ C. and salinities of $> 34{\cdot}5‰$.

The *Atlanto-Scandian group* has a more northerly distribution, extending from the Norwegian coast to Iceland, whereas the *Hiberno-Calédoniens group*, of which the Minch spring spawners are a typical member, is distributed along the continental shelf to the west of Scotland and Ireland. It is suggested, however, that some mixing of the two groups takes place in Shetland waters and in the northern North Sea.

The mean vertebral number of the *Atlanto-Scandian group* is consistently higher than that of the Minch spring spawners. Runnström (1941 a) gives the mean vertebral number of Norwegian spring spawning herring as 57·32. Friðriksson (1956), however, obtained vertebral means for Norwegian spring spawners at Iceland which ranged between 57·12 and 57·19. These values obtained by Friðriksson are very similar to the vertebral means of the Norwegian "large" herring which appear off the coast of Norway in December and January and which have a mean of 57·18 (Runnström, 1941). The Minch spring spawners have lower mean vertebral numbers, which range between 56·93 and 57·03.

Any subdivision of the spring spawning herring population in the North Atlantic must present difficulties in deciding the affinities of each spawning group within the population, but it is considered that Le Gall's proposed subdivision of the spring spawners of the North Atlantic, into the *Atlanto-Scandian* and *Hiberno-Calédoniens groups*, is sound; further evidence produced in this paper supports Le Gall's hypothesis.

B. The Minch Autumn Spawners

1. Spawning grounds

The location of the main spawning centres of the Minch autumn spawning herring has presented some difficulties. There is no fishery in the autumn for spawning herring such as occurs along the mainland coast in the spring.

From Table 10, in which the maturities of Minch samples between June and September are given, the development of the gonads of the autumn spawners can be followed from stage II in June to stages IV and V in August, while in September spents and recovering spents appear in the catches in large numbers. Herring in stage VI are conspicuously few in number throughout the Minch during this period. It would appear therefore that the majority of autumn spawners leave the fishing ground for spawning between the stages IV and V. The results, however, of herring larval surveys carried out on the west coast of Scotland (Baxter, 1954) indicate that autumn spawning in the Minch is spread over a wide area extending from the Butt of Lewis to the Island of Mull.

Centres of high density of newly hatched larvae were obtained in the following regions (Fig. 5):—

1. On the south and west coasts of the Island of Mull.
2. On the north coast of Skye in the same region as spawning herring were taken in 1955.
3. Off the Butt of Lewis.
4. On the mainland coast in the vicinity of the Islands of Handa and Bulgie.

Spawning appeared to take place earlier in the north than in the south and the period of spawning extended from August to the beginning of October.

Table 10
Percentage maturities of samples from Minch

	Stage...	I	II	III	IV	V	VI	VII	VII-II	Number of fish
	Year				June					
Lewis Grounds	1953	13·7	**69·2**	3·4	1·6	0	0	0·2	11·9	445
	1954	32·5	**46·5**	1·0	0	0	0	0	0	200
	1955	8·0	**46·7**	3·5	2·0	1·0	0	0	38·7	199
Mainland Grounds	1954	43·2	**43·1**	3·8	0·3	0·5	0	0	8·8	444
	1955	8·7	**49·3**	2·0	1·0	1·0	0	0	38·7	150
					July					
Lewis Grounds	1953	14·8	**52·2**	17·0	6·8	8·4	0	0	0·9	454
	1954	36·5	**43·7**	8·7	3·9	6·3	0	0	0·9	460
	1955	8·5	**45·0**	**22·0**	13·6	7·3	0·7	0	2·9	449
Mainland Grounds	1952	19·2	**32·3**	13·6	17·7	11·6	0	0	5·6	243
	1955	0	**24·0**	**20·0**	**20·0**	**32·0**	2·0	0	2·0	50
					August					
Lewis Grounds	1952	21·7	**27·3**	**20·8**	16·9	8·7	0	1·3	4·5	231
	1953	28·7	12·0	16·2	**27·6**	14·1	0	0	1·6	192
	1954	23·1	14·5	10·2	**22·6**	**24·5**	3·8	0·2	1·0	420
	1955	8·7	17·3	**24·9**	**25·1**	11·5	10·0	0·4	2·2	550
Mainland Grounds	1953	10·4	19·8	11·4	11·9	19·8	1·0	11·4	14·4	202
					September					
Lewis Grounds	1951	0·9	0	0·5	0·9	1·4	0	**96·4**	0	220
	1952	17·0	11·2	24·5	10·7	2·0	0	14·2	**20·0**	736
	1953	33·3	12·4	8·7	8·1	4·3	0·4	17·6	15·1	700
	1954	21·9	17·3	5·4	3·4	1·4	0	**20·5**	**30·1**	498
	1955	23·9	18·8	4·0	8·0	2·3	8·0	7·5	**28·3**	400
Barra Grounds	1954	22·0	12·4	7·2	4·0	1·6	0	**42·4**	10·4	250

2. Race characters of Minch autumn spawners

(a) *Vertebral numbers.*

In establishing the race characters of any stock the normal practice is to begin with the characters of spawning herring and to use this standard as a comparison for the groups in the pre-spawning and post-spawning stages. Unfortunately in the Minch we are limited to one sample of spawning herring which was obtained by a ring-net vessel working off the north coast of Skye on 30. August 1955. The mean vertebral number of this sample was 56·45 which is very similar to the values given for neighbouring autumn spawning stocks. Wood (1936) found that the mean vertebral count of Minch autumn spawning herring ranged from 56·42—56·48, while for Shetland he gives 56·36—56·51 and for the Scottish north-east coast fishery 56·40—56·45. Hsüeh (1939) working on the race characters of the Manx autumn spawners obtained means ranging from 56·38—56·54. The distribution of vertebrae and means of the main groups, from samples of autumn spawners taken throughout the year, are given in Table 11.

It will be seen that the mean vertebral numbers ranged between 56·40 and 56·52. It is clear, therefore, that the distribution of vertebrae and the mean vertebral number cannot be used as a character to distinguish the Minch autumn spawners from other neighbouring autumn spawning groups.

(b) *Length of formation of first winter-ring* (l_1).

The distributions of l_1's for different age-groups during 1954 and 1955, given in Table 12, show that the values obtained were spread over a considerable range from 7—19 cm., although the majority of observations lay between the 11 and 15 cm. groups. The modes occurred mainly in the 13 and 14 cm. groups. The 1952 brood appearing as 2-ringed fish in 1955 had a mode of 15 cm. Greater variation in the distribution of l_1's was noticeable in the older age-groups, suggesting that although the new recruits to the stock might be derived from one nursery area, the older fish may have been derived from two or more nursery areas.

A comparison of the l_1 material from the Minch and from the Scottish east coast autumn spawners given in Table 13 shows that the Minch autumn spawning herring have lower modes and means for the same age-group and this is particularly noticeable in the younger age-groups where the modes differ by as much as 2 cm.

The distribution of l_1's of the Kessock halflin herring presented in Table 14 is more similar to the Minch l_1

Table 11
Distribution of vertebrae (%) of Minch autumn spawners

1953

Period	January-March	April-June		July-September		October-December	
Year-class	1949	1950	1949	1950	1949	1950	1949
No. of rings	3	2	3	2	3	2	3
Vertebrae							
59	—	0·50	—	—	—	—	0·33
58	3·36	3·90	3·42	5·30	7·34	3·09	4·34
57	42·95	46·34	38·46	38·41	32·20	43·09	45·15
56	50·00	42·93	52·99	54·97	55·37	50·10	45·15
55	3·69	6·34	5·13	1·32	5·08	3·71	5·02
Total	298	205	117	151	177	485	299
Mean	56·46	56·49	56·40	56·48	56·42	56·46	56·50

1954

Period	January-March		April-June			July-September			October-December		
Year-class	1950	1949	1951	1950	1949	1951	1950	1949	1951	1950	1949
No. of rings	3	4	2	3	4	2	3	4	2	3	4
Vertebrae											
59	—	—	—	—	—	0·25	—	—	0·20	—	—
58	3·22	5·77	4·07	3·23	9·32	5·54	3·23	4·63	4·67	3·86	4·07
57	41·80	41·54	45·12	40·86	38·14	40·30	48·39	44·44	42·68	43·80	47·51
56	53·05	50·00	48·37	52·15	46·61	48·61	46·08	48·15	47·56	48·48	45·24
55	1·93	2·69	2·44	3·76	5·93	5·04	1·84	2·78	4·88	3·86	3·17
54	—	—	—	—	—	0·25	0·47	—	—	—	—
Total	311	260	246	186	118	397	217	108	492	363	221
Mean	56·46	56·50	56·51	56·44	56·50	56·47	56·52	56·51	56·48	56·48	56·52

Table 13
l_1 distribution of Scottish east coast autumn spawners[1])

	1954		
Year-class	1951	1950	1949
cm. Rings...	2	3	4
8	—	2	1
9	—	0	3
10	—	2	11
11	3	3	25
12	4	10	27
13	16	19	35
14	21	**27**	32
15	**23**	**27**	**36**
16	16	23	25
17	19	14	11
18	6	14	5
19	6	3	1
20	1	1	—
Total	152	149	228
Mean	15·16	14·93	13·50

data than to the adult stock of autumn spawners of the Scottish north-east coast. HSÜEH (1939) found modes ranging between 10 and 13 cm. for different age-groups in the Manx herring.

3. Length composition

In Table 15 the mean lengths are given for each of the main age-groups of autumn spawners in the Minch. The means obtained in the Scottish north-east coast fishery shown in Table 16 A (PARRISH) are very similar. The data given by BOWERS (1955) for the Manx autumn spawners (Table 16 B), however, show that the mean lengths at each group are consistently lower than both the Minch and Scottish east coast autumn herring.

4. Age composition

In Figure 6 the age composition of the Minch autumn spawners is given for the periods April to September and October to March. With the excep-

Table 14
l_1 distribution of Kessock halflins[1])

Date	Year-class	cm. 7	8	9	10	11	12	13	14	15	16	17	18	Total	Mean
20.11.51 ..	1949	—	—	1	4	15	30	34	**49**	44	45	10	2	233	14·91
16.12.52 ..	1950	—	1	7	9	23	24	33	**51**	43	19	2	2	214	13·38
12.3.54 ...	1951	1	3	4	15	**19**	8	16	13	10	—	—	—	89	11·93
3.3.55 ...	1952	—	—	—	3	23	38	**45**	31	15	11	3	—	169	13·08

[1]) From PARRISH, personal communication.

Table 12
l_1 distribution of Minch autumn spawners

1954

Period	January-March		April-June			July-September			October-December		
Year-class	1950	1949	1951	1950	1949	1951	1950	1949	1951	1950	1949
No. of rings	3	4	2	3	4	2	3	4	2	3	4
cm.											
7	—	—	—	—	—	—	—	—	—	2	1
8	—	1	1	4	1	—	1	—	1	6	—
9	2	2	4	8	2	5	7	—	4	14	3
10	7	8	4	11	5	10	17	3	16	26	10
11	20	18	13	15	11	31	13	6	29	41	21
12	25	24	22	**33**	**27**	44	17	10	69	55	24
13	**51**	**38**	38	22	16	67	**30**	19	**117**	**65**	38
14	44	26	**40**	**30**	**26**	**72**	28	**21**	88	61	**53**
15	29	28	23	17	19	42	11	**21**	61	35	37
16	9	14	5	8	19	12	9	5	17	6	13
17	4	1	1	3	3	8	4	4	4	2	4
18	2	—	2	0	1	—	1	—	2	—	—
19	—	—	—	1	—	—	—	—	—	—	—
Total	193	160	153	152	130	291	128	89	408	313	203
Mean	13·32	13·19	13·22	12·72	13·47	13·23	13·01	13·71	13·22	12·50	13·36

1955

Period	January-March			April-June		July-September			October-December		
Year-class	1951	1950	1949	1951	1950	1952	1951	1950	1952	1951	1950
No. of rings	3	4	5	3	4	2	3	4	2	3	4
cm.											
7	—	1	—				—	—	—	—	—
8	1	4	—	—	—	1	1	4	—	—	2
9	3	21	3	3	1	3	13	8	1	4	6
10	5	36	16	7	3	9	29	11	4	10	12
11	16	31	13	21	8	16	49	12	9	10	11
12	35	27	26	28	9	27	82	13	9	41	12
13	**56**	43	33	**38**	10	29	**86**	11	18	**43**	**15**
14	47	45	**43**	33	9	41	79	11	23	34	13
15	19	36	33	20	**14**	**51**	40	12	**24**	27	7
16	9	6	15	3	8	26	13	3	17	6	4
17	2	7	2	1	5	10	2	2	8	3	4
18	—	—	1	—	2	7	1	0	4	3	2
19	—	—	—	—	—	1	—	1	1	—	—
Total	193	257	185	155	69	221	395	88	118	181	88
Mean	13·11	12·45	13·30	12·92	12·77	13·90	12·71	11·90	14·16	13·09	12·56

tion of 1951 and the early part of 1952, the Minch autumn spawners during 1951 to 1955 were composed mainly of young fish with between 2 and 5 winter-rings on their scales. A comparison of the age compositions in the two periods April to September and October to March shows that the age compositions of the summer and winter fisheries were fairly similar.

Discussion

The race characters of the Minch autumn spawners are similar to those obtained in neighbouring autumn spawning stocks. The mean vertebral numbers range between 56·40 and 56·52 and therefore can't be used as a character to distinguish the Minch autumn spawners from other stocks. The average length of each Minch age-group was similar to that of the autumn spawners of the Scottish north-east coast, but was consistently higher at each age-group than the values obtained by Bowers (1954) for Manx autumn spawners. The distribution of l_1's and mean l_1 values showed some differences from the Scottish north-east coast autumn spawners especially in the younger age-groups, where modes and means were 1—2 cm. higher than those obtained in the Minch. The l_1 values for the Kessock halflins, however, which are considered to provide some of the recruitment to the east coast fishery, were more similar if somewhat lower than those in the Minch.

The results from tagging experiments in the Minch during the period 1951—55 have been disappointing on account of the small number of returns. With the exception of one herring which was tagged in the North Minch in August 1953 and recaptured on the Fladen

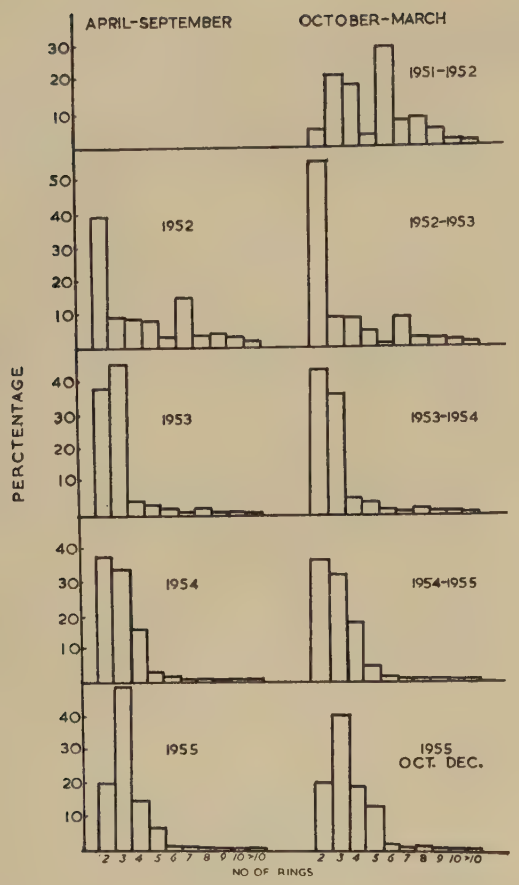


Figure 6. Age composition of Minch autumn spawners.

Ground in August 1954, all the other returns have been from the Minch itself. Such results as have been obtained suggest that there is a free interchange between the North and South Minch. A recapture in the Minch which is of special interest, was of a herring tagged off Peterhead in August 1954 and recaptured in the North Minch in November of the same year. It would appear, therefore, that some interchange may take place between the autumn spawners of the Minch and the North Sea.

The fishery for autumn spawners in the Minch is unique for Scottish waters since it is in progress almost continuously throughout the year. The fishery, however, is most productive between November and March when the total landings and catch per landing are higher than in other months. The summer fishery is dependent to a large extent on the size of the new recruit brood coming into the stock. This fact was demonstrated between 1951 and 1955 when in the three years of good recruitment, between 1952 and 1954, the summer fishery was most productive, while in 1951 and 1955 the recruitment was poor and also the summer fishery.

Table 15
Mean lengths (cm.) of main age-groups of Minch autumn spawners
(Number of fish in brackets)

January-March

Year	Rings...	(2+)3	(3+)4	(4+)5
1953		25·83 (310)	—	—
1954		25·29 (185)	26·82 (199)	—
1955		25·26 (221)	26·72 (304)	27·85 (202)

April-June

Year	Rings...	2	3	4	5
1953		24·23 (207)	26·07 (120)	—	—
1954		24·11 (251)	25·84 (194)	27·37 (146)	—
1955		24·11 (46)	25·97 (255)	27·34 (96)	28·37 (38)

July-September

Year	Rings...	2	3	4	5
1953		25·27 (154)	26·87 (183)	—	—
1954		24·81 (419)	26·68 (275)	28·15 (124)	—
1955		25·00 (290)	26·79 (479)	27·96 (134)	28·87 (61)

October-December

Year	Rings...	2	3	4	5
1953		24·95 (504)	26·82 (312)	—	—
1954		25·08 (500)	26·61 (381)	27·82 (217)	—
1955		25·36 (134)	27·23 (217)	28·02 (102)	28·80 (82)

In early spring there appears to be a movement of adult herring out of the Minch, since the concentrations of herring are small during April and May. This is probably a feeding migration and it is of importance to note that particularly high concentrations of *Calanus* are found west of Orkney and also between Barra Head and the north coast of Ireland during this period (Gibbons, 1936). This spring emigration is followed in the summer by an immigration of some adult autumn spawners into the Minch. These herring appear to spawn in the Minch during the autumn.

The further increased productivity of the fishery, which takes place during the late autumn and winter months, suggests that the autumn spawning units which are already in the Minch have been augmented by representatives of another autumn spawning group or groups which may not spawn in the Minch but spend the winter there as recovering spents.

Table 16 A
Mean lengths (cm.) of main age-groups of Scottish east coast autumn spawners[1])
(Number of fish in brackets)

Year	Rings...	May-September 2	3	4	5
1953		24·54 (2,974)	26·37 (2,167)	27·00 (609)	28·09 (515)
1954		24·69 (3,700)	26·92 (1,438)	28·12 (1,013)	28·71 (325)
1955		24·18 (2,842)	26·81 (863)	28·68 (332)	29·34 (305)

[1]) From PARRISH, personal communication.

Table 16 B
Mean lengths (cm.) of main age-groups of Manx autumn spawners

Year	Rings...	2	3	4	5
1954	June	23·24 (71)	24·46 (68)	26·08 (18)	—
	July	34·33 (104)	25·48 (123)	26·38 (55)	27·35 (33)
	August	24·39 (104)	25·81 (162)	27·02 (66)	27·68 (35)
	September	24·14 (113)	25·87 (83)	26·96 (47)	27·89 (21)

Conclusions

The data presented in this paper indicate that the Minch spring spawning herring have certain meristic and behaviour characteristics which distinguish them from the Atlanto-Scandian spring spawners. It is, therefore, considered that LE GALL's subdivision of the spring spawning herring of the North Atlantic into Atlanto-Scandian and Hiberno-Calédoniens groups is sound.

It is suggested that the autumn spawners fished in the Minch are members of more than one group and these groups are broadly defined as follows:—

(a) A local group which is present in the Minch during all or most of the year and which spawns there.

(b) A group (or groups) which does (do) not spawn in the Minch but which spends the winter there as recovering spents.

Summary

Herring fishing in the Minch is in progress almost continuously throughout the year but there are two main periods of high activity; November to March and June to September. The late autumn and winter fisheries are generally more productive than the summer fishery.

The Minch herring population is composed of a mixture of spring and autumn spawners. The racial characters of each group are described and compared with those of neighbouring stocks of spring and autumn spawners.

It was found that the mean vertebral number of the Atlanto-Scandian group was consistently higher than that of the Minch spring spawners and that the Atlanto-Scandian group spawn in conditions of lower temperature and salinity.

LE GALL's subdivision of the spring spawning herring of the North Atlantic into Atlanto-Scandian and Hiberno-Calédoniens groups is considered sound.

The racial characters of the Minch autumn spawners are similar to those of neighbouring autumn spawning stocks. It appears that in early spring there is a movement of adult autumn spawners out of the Minch and that during the summer some of these return and spawn there. In November this stock is augmented by representatives of another group or groups of autumn spawners which probably do not spawn in the Minch but spend the winter there as recovering spents. Tagging results indicate that there is some interchange of autumn spawners between the Minch and the North Sea.

It is suggested therefore that the autumn spawners fished in the Minch are members of more than one group and these groups are broadly defined as follows:—

(a) A local group which is present in the Minch during all or most of the year and which spawns there.

(b) A group (or groups) which does (do) not spawn in the Minch but which spends the winter there as recovering spents.

References

BAXTER, I. G., 1954. Ann. Biol. Copenhague, **10**: 150—51.

BOWERS, A. B., 1955. "Age and size of Manx herring in 1954". Rep. Mar. Biol. Stat. Pt. Erin, **67**: 31—33.

BOWMAN, A., 1923. "Spawny haddocks". Sci. Invest. Fish. Scot., 1922, 4, 15 pp.

EINARSSON, H., 1951. "Racial analysis of Icelandic herring by means of otoliths". Rapp. et Proc.-Verb., **128** (1): 55—74.

FRIÐRIKSSON, Á., 1953. Ann. Biol. Copenhague, **9**: 164—67.

— 1956. Ibid., **11**: 114—18.

GIBBONS, S. G., 1936. "*Calanus finmarchicus* and other copepods in Scottish waters in 1933". Sci. Invest. Fish. Scot., 1936, 2, 37 pp.

HEINCKE, F., 1898. "Naturgeschichte des Herings". Abh. Dtsch. SeefischVer., **2**, 223 pp.

HSÜEH, F., 1939. "A study of Manx herring shoals". Rapp. et Proc.-Verb., **111**: 55—83.

JOHANSEN, A. C., 1919. "On the large spring-spawning sea herring (*Clupea harengus* L.) in the north-west European waters". Medd. Komm. Havunders., Ser. Fisk., **5** (8): 1—56.

Lea, E., 1910. "On the methods used in herring investigations". Publ. Circ. Cons. Explor. Mer, 53.

Le Gall, J., 1935. "Le hareng *Clupea harengus* Linné. 1. Les populations de l'Atlantique Nord-Est". Ann. Inst. Océanogr., **15**, 215 pp.

Lissner, H., 1934. "On the races of herring". J. Cons. Int. Explor. Mer, **9** (3): 346—64.

Parrish, B. B., & Sharman, D. P., 1956. "Some remarks on objects and methods used in herring "racial" investigations with special reference to otolith studies". This volume, p. 66.

Runnström, S., 1941a. "Racial analysis of herring in Norwegian waters". Fiskeridir. Skr., **6** (7) 110 pp.

— 1941b. "Quantitative investigations on herring spawning and its yearly fluctuations at west coast of Norway". Ibid., **6** (8) 71 pp.

Schnakenbeck, W., 1927. "Rassenuntersuchungen am Hering". Ber. Dtsch. Komm. Meeresforsch., **3** (2): 95—205.

Storrow, B., 1923—40. "Herring investigations". Rep. Dove Mar. Lab., 1923—40.

Wood, H., 1923. "Observations on the Scottish summer herring fishing of 1922". Sci. Invest. Fish. Scot., 1923, 2, 42 pp.

— 1930. "Scottish herring shoals: pre-spawning and spawning movements". Ibid., 1930, 1, 71 pp.

— 1936. "Race investigations of the herring population of Scottish waters". Ibid., 1936, 3, 52 pp.

— 1937. "Movements of herring in the northern North Sea". Ibid., 1937, 3, 49 pp.

— 1951. "Observations on the value of l_1 in herring investigations". Rapp. et Proc.-Verb., **128** (1): 39—46.

12.

Racial Investigations on Herring, Especially Adult Herring in the Skagerak

By Aage J. C. Jensen

The solution of the question of the origin of the herring in the Skagerak encumbers the difficulty that the racial characters, especially of the North Sea autumn spawners, are not sufficiently known. Basis diagrams VS—VP and VS—K_2 published in 1951 have been revised by including the later statements of the racial characters; but only a few of the published data refer to actual spawning stocks (maturity VI only), and therefore these basis diagrams are provisional. The migrations just before and just after spawning may be rather long, as proved by some of the marking experiments, and therefore the inclusion in the basis diagrams of racial characters of herring of maturity V or VII may be precarious.

The herring caught off Lowestoft afford an example hereof.

From the racial analyses it is evident that they do not belong to a uniform stock, but that the composition of different races fluctuates very much from year to year and often in one and the same year. It cannot be proved from the age composition that only one race is included in a catch as the age composition in different races may of course be alike.

Sometimes the racial characters of spawning herring of mixed samples from very extensive fishing grounds are published and it cannot therefore be ascertained to which spawning ground they belong.

Up till now it seems to have been established that the characters VS, VP, or K_2 of a race do not vary much and that they are to be considered as genotypical. Most probably the choice of a spawning ground with special physical characteristics is a basic genotypical character but the salinity and temperature are doubtless two of the most important components. The temperature just after hatching of the larvae may influence phenotypically the number of vertebrae somewhat. From the data published by Bückmann (1950) it is seen that in 1929—35 a difference of 1° C. roughly corresponded to a difference of —0·1 VS, but from the figures published in this volume it appears that 1° C. corresponds to about —0·01 VS.

Naturally the growth during the first months must also partly be determined genotypically in so far as the spawning season is mainly fixed genotypically, but we know that the spawning season may fluctuate by, for example, one month according to the temperature and that the growth conditions for the larvae and young herring (temperature and food) may differ very much from one year to another. Therefore the L_1 is mainly a phenotypical character, although it may be used for a rough discrimination between, for instance, spring and autumn spawners.

Experience has shown that the geographical position of a spawning ground of a race of herring may vary somewhat.

This is particularly characteristic of the spring spawners. For instance, herring with the same VS, VP, and K_2 may spawn off the southern and western shores of the Kattegat and in the Belts, or even in the western Baltic (in the western Baltic there is also a race of spring spawners, but it has never been found spawning in the Belts or in the Kattegat).

It is important to note that a great change in the meristic characters of a herring race has been stated for the Norwegian winter/spring herring and for the same race off Iceland and the Faroes, but nowhere else. The values found here during 1888—1924 by Heincke, Dahl, and Johansen have not been shown in the basis diagram. They are the following:— VS = 57·3—57·7; VP = 23·3—24·7; K_2 = 13·7—14·3. In 1915—24 they were found by A. C. Johansen in samples from northern Iceland (and in 1925 this

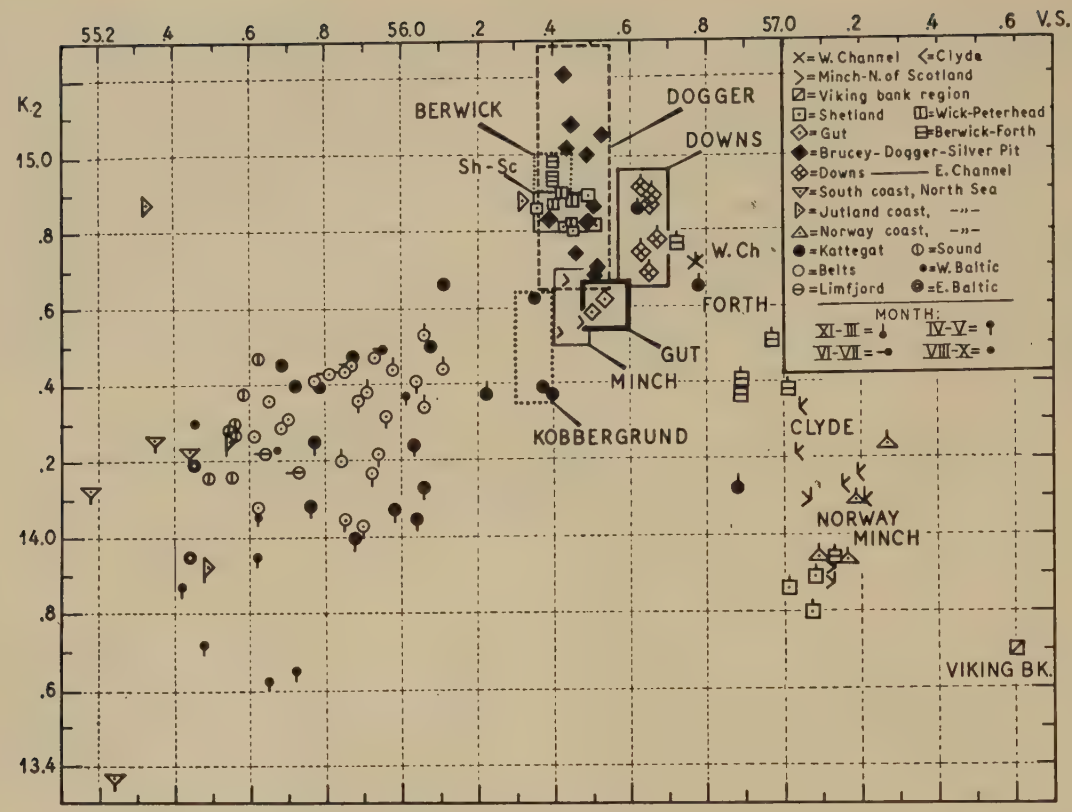


Figure 1.

race was supposed to be spawning at Selvogsbanki, S.W. Iceland, in 100 metres depth; but 34 specimens only were examined by A. C. Johansen).

For the years 1932—36 Runnström (1941) found a VS of 57·0—57·5 for the 1918—32 year-classes with a decreasing trend during these years. He ascertained a VS of 57·3—57·4 in about half of the samples of herring in maturity stages VI—VII in the spawning area north of Cape Stat and a VS of 57·3—57·5 in most of the samples in the main spawning area Bergen—Lindesnes. My own investigations have shown that VP is now 24·3—24·4 and K_2 13·9—14·3 in samples having vertebral counts of 57·1—57·3.

It might seem that herring having a very high VS (57·6) have spawned in recent years on the Viking Bank, as found by Schubert (1954), but it should be noticed that the sample investigated by Schubert had a K_2 at the lower limit of the former characters of the Norwegian winter/spring spawners and that the VP is not known.

The cause of the change of the winter/spring spawners off the Norwegian coasts may be that the stock of the former deep-water winter/spring herring off the Norwegian coast has become scarcer and that another stock of herring spawning at somewhat less depths has now become more frequent here, or, possibly, the racial characters of the stock have changed in consequence of a higher water temperature.

Altnöder (1928) has stated that the racial characters of the herring spawning in the Schlien (western Baltic) now differ from those found by Heincke and refers to a communication by Dr. Neubaur that the racial characters here have not been constant in recent years. In view of the rather few samples from this fjord, investigated by Heincke, and the fact that the meristic characters may vary considerably in estuarine waters it is dubious if they have actually been more constant in Heincke's time than now.

A large material is necessary in order to determine the distinctive characters of different year-classes in a certain spawning community or race.

From a glance at the basis diagrams, Figures 1 and 2, it is evident that the vertebral counts alone allow a separation of some of the large race groups, such as the Kattegat—Belt Sea—Baltic group having a VS of 55·40—56·15, the group of North Sea autumn spawners (VS = 56·35—56·56), and the winter/spring spawners (VS = 56·60—57·30). In some cases each of the major groups may be subdivided, particularly when we combine the vertebral counts with our knowledge of the spawning season (or L_1).

But it is seen at once that the VS—VP and VS—K_2

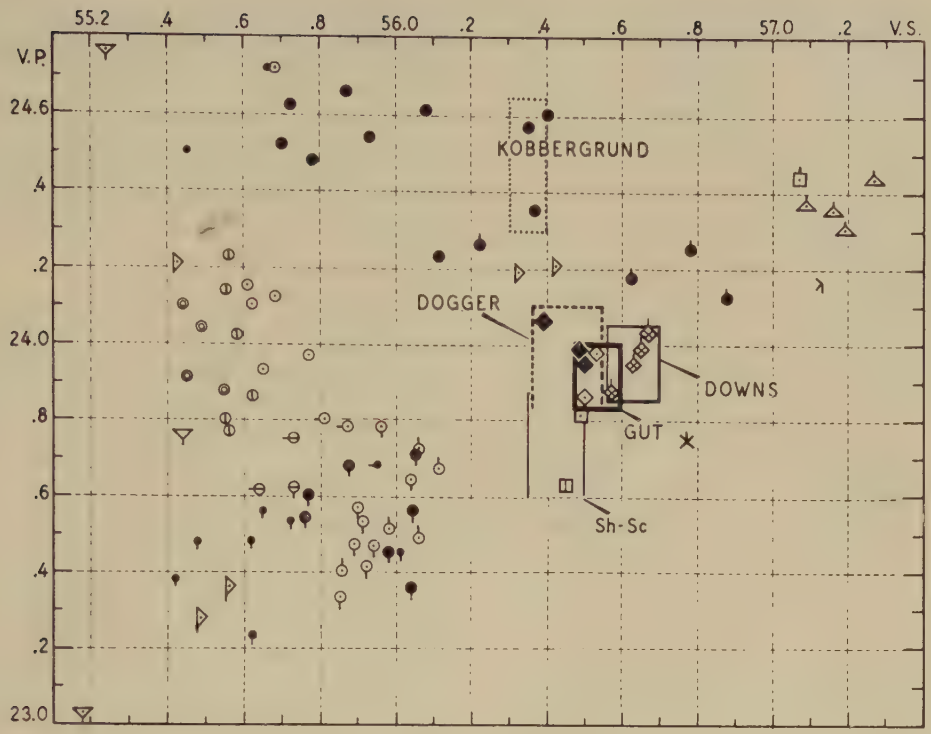


Figure 2.

diagrams give far better means for a discrimination of local races. The symbols for the samples of herring spawning in a certain locality and at a certain season are centred in distinct clusters in most cases. A particularly pronounced exception is afforded by the range of K_2 of the mature herring caught in the Gut—Dogger Bank—Silver Pit—English coast region; this range is astonishingly wide but this is doubtless due mainly to insufficient information of the racial characters of herring of maturity stage VI on the different spawning grounds. From the data published we cannot separate the samples into groups belonging to the different spawning grounds within this area.

The distribution on the VS—VP diagram of the symbol for the coastal spring spawners from the southern North Sea form a peculiar exception from the rule of clusters. In one of the samples investigated by Hempel (1953) the VP is 23·77 (from the Ems) and in another (from the Elbe) it is 24·77. In both samples it is anomalous and it would be very interesting to know the reason. Also the K_2 of the Elbe sample is astonishing, and it is very much lower than, for example, for the spring spawners of the western Baltic.

The basis diagrams show that in the waters inside the Scaw VP combined with VS show much more clearly the difference between autumn and spring spawners than K_2 combined with VS. It is seen from the diagrams that in the Kattegat-Belts-Baltic region the VP is comparatively higher for the autumn spawners than for herring spawning in other seasons, and that the summer spawners have VP at the highest limit for the spring spawners. In the VS—K_2 diagram the spawners from the different seasons overlap to some degree but we may yet be certain that herring with a specially low K_2 are spring spawners. Summer, autumn, and winter spawners have a comparatively high K_2.

Spent herring in the Skagerak

These herring are shown in the diagram on Figure 3. For each season the mean of the samples have been shown and in some cases there is a wider spread of the single samples than shown in the figure indicating that the stock is not always homogeneous.

It is seen that VS is 56·4—56·5, VP 23·65—24·10, and K_2 14·8—15·0 except in three samples. A sample investigated in 1887 by Heincke had a lower K_2 and a higher VP which clearly marks it out as Kobbergrund herring. The value of VS is a little higher for this race, but it is explained by the small number (57) investigated. A sample from 1923 differs from the main grouping by a slightly lower VS and a low VP. The deviations are so small that it may be considered as belonging to the herring spawning off the Scottish coast. A sample from 1905 differs by a high K_2 indicating that it belongs to the Dogger Bank group.

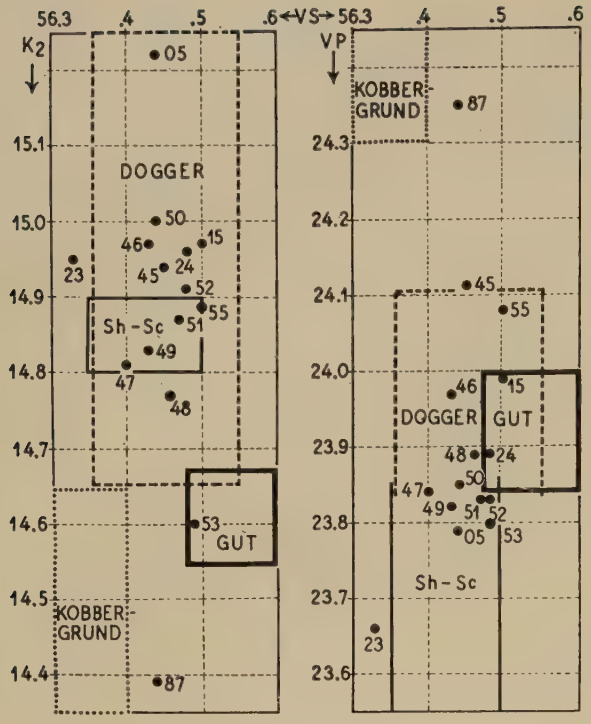


Figure 3.

The vertebral counts indicate that the herring in the cluster are either Shetland-Scottish or Dogger Bank autumn spawners. According to the K_2 all of them may as well be Shetland-Scottish autumn spawners. Especially the samples from 1915, 1924, 1946, 1950, and perhaps 1945, differ from the Shetland-Scottish herring, but the samples are too small to exclude that the difference is due to the standard errors. Our knowledge of the VP of the various races is very limited and the validity of the numerical values of this character is therefore uncertain; it seems that most of the samples according to this character apply to both races (or race groups). The samples from 1915 and 1946 seem to be excluded from the Shetland-Scottish group also by this character and included in the Dogger Bank group, and the sample from 1955 seems to belong to the same group owing to this character.

The result of the investigation is that the spent herring in the Skagerak may belong to rather different spawning grounds from east of Shetland to the Dogger Bank, and that the composition of the Skagerak stock according to their origin may vary in the different years.

Full herring

Full herring in maturity stage V may constitute a part of the adult herring living in the south-eastern Skagerak (the main Danish herring-trawling grounds). In winter they are sometimes rather plentiful here after periods with strong westerly or north-westerly winds; their vertebral count is about 57·0, VP 24·0—24·4, and K_2 is about 14·3 in some of these herrings. Their length lies between 26 and 31 cm. and they belong to the Atlanto-Scandian winter spawners, and most of them undoubtedly to the groups spawning in the Skagerak and the northern Kattegat. In November 1955—January 1956 herring of maturity stage V were comparatively abundant in the trawl catches off Hirtshals. Their racial characters were the following:— VS = 56·8, VP = 24·3, and K_2 = 14·9 (106 specimens); their average length was 28—31 cm. In the diagrams they are nearest to a sample of spring spawners from the Firth of Forth but they may possibly originate from spawning grounds in the Skagerak for which we do not know the values of VP and K_2.

In the summer full herring from the western part of the North Sea and from the northern Kattegat may be caught in the Skagerak by trawl, but the quantity of adult herring is comparatively very small at this season.

During spring full herring may form part of the catch in pound nets off the Scaw, but these herring will quickly migrate to the east coast of Jutland, in the central Kattegat, and to the Limfjord for spawning, as shown by racial investigations and by marking experiments.

13.

Fecundity of Baltic Herring

By R. Kändler *and* S. Dutt

The Baltic Sea, as the largest brackish sea in the world, and because of its peculiar physical and chemical characteristics, offers a milieu which in many ways is very different from any other; in comparison with the adjoining and connected North Sea, it is definitely not so favourable for the fish populations. Its distinctive features such as the low salinity, the temperature, and the scarce food supply are bound to exert a considerable influence on the fish, and the influence of these factors on growth and development has been emphasized by a number of authors. In this connexion, Franz (1910), Simpson (1951), and Kändler & Pirwitz (1957) have shown that the Baltic races of flatfish have a considerably higher fecundity than those of the North and Barents Seas, apparently to make up for the higher rate of mortality among eggs and fry.

The first work on the fecundity of herrings from the Baltic Sea was published by Jenkins (1902). In 8 autumn spawners from the western Baltic studied (he gives only the length of the fish excluding the tail fin in this sample: 14·4 to 21·5 cm.), the fecundity varied between 13,000 and 65,400, and in 5 spring spawners from the same area, ranging in total length from 22·1 to 25·4 cm., it varied between 26,000 and 40,000. He noted the relation between the fecundity and the age and size of the fish. In his work he also refers to results obtained by previous workers in other areas. Accordingly Bloch (quoted by Kröyer, 1828—54) had estimated the number of eggs to exceed 68,000. On the other hand Day believed it to vary between 10,000 and 30,000. Matthews (1885) believed this to be underestimated and that the fecundity was in the region of 48,000. Huxley (1881), however, assumed even 30,000 to be too much. Benecke (1886) estimated it to vary between 40,000 and 100,000. Fulton (1890) recorded that there is always a great variation within the same species. In 16 spring spawners from Scottish waters examined by him, the fecundity varied between 21,500 and 47,466. Jenkins attributed the great difference in the results obtained by previous workers, which ranged from 10,000 (Day) to almost 100,000 (Benecke), to the difference in the ages of the fish studied and to the fact that fish with the lowest fecundity were probably spawning for the first time.

Later on, Farran (1938) estimated that the fecundity of autumn spawners from the north and east coasts of Ireland ranges from about 25,000 to 128,000 for fish differing in length from 22 to 31 cm., and from about 8,000 to 82,000 (approximately) for spring spawners differing in length from 21 to 34 cm. from the north, south, and east coasts of Ireland. He estimated the number of ova to be proportionate to $L^{4.5}$ for both spring and autumn spawners.

The next worker to study the fecundity of the herring was Hickling (1940). In 136 autumn spawners from the southern part of the North Sea (East Anglia) ranging in length from 21·5 to 29·5 cm., the fecundity ranged from 12,223 to 36,599. He obtained the following equation as the mathematical expression of the relationship between the number of eggs and the length of fish:—

$$F = 0.2954 \cdot L^{3.465}$$

He noted that his results were in agreement with those of Fulton (1891), whereas the results obtained by Mitchell (1913) for summer spawners exceeded three times those obtained by Fulton. Hickling

believes that fecundity is adapted in some way to the seasons and indicates the order of fecundity to be as follows: least in spring spawners, more in winter spawners, still more in autumn spawners, and the highest fecundity in summer spawners.

Methods of counting herring eggs

Different methods have been employed by previous workers for the study of the fecundity in the herring. JENKINS used the following method: after carefully weighing small pieces from different parts of the ovary, and cooking them for 10—15 minutes, he spread the ova on a slide and counted them. He then estimated the fecundity for the whole weight of the ovary. FARRAN (1938) weighed the ovary, counted the number of ova and measured the average diameter of the ova in 3 individuals. From this he found that there is a relationship between number of eggs, weight of the ovary, and the diameter of the ova, so that he was able, only by measuring the diameter of ova and the weight of the ovary, to make up the total number of eggs in the ovary of a fish, by the formula:—

$$\text{Number of eggs} = \frac{\text{weight of ovary} \cdot x}{\text{diameter}^3}$$

He obtained an average value of 2,150 for x from three fish in which he actually counted the eggs. HICKLING (1940) estimated the fecundity of the herring from East Anglia by modifying the method used by RAITT (1933) for haddock; the ovaries, preserved and hardened in formalin, were cut into pieces and shaken vigorously with water in a stoppered jar. They were then counted according to the method used by NUTTALL (1913) in counting the eggs of ticks.

Material and methods used in the present investigation

The material for the present study on the fecundity of herrings was collected in the period March—October 1955 on the Kiel fish market, where fishes are landed not only from the different parts of the Baltic but also from the North Sea. The method employed was as follows: after each fish had been measured for the total length and weight and the weight of the ovaries, the otoliths and a few well developed scales were removed for estimating the age. The ovaries were then preserved in GILSON's fluid, as modified by SIMPSON (1951): 100 ml. 60% alcohol, 880 ml. water, 15 ml. 80% nitric acid, 18 ml. glacial acetic acid, 20 g. mercuric chloride. Although this fluid has not been previously used for the ovaries of herrings, it was found to be very satisfactory, especially after the ovaries had remained in the fluid for a couple of weeks. For better penetration of the fluid, the ovaries were cut into several pieces by transverse incisions. After immersion of the eggs in the fluid, the bottle was immediately shaken a couple of times so that the eggs were freed from the ovarian membranes and the connective tissues to which they are attached. For counting the eggs, we used the method employed by R. KÄNDLER and W. PIRWITZ (1957) in their work on the fecundity of flatfish: the ovaries, preserved in GILSON's fluid for a couple of weeks (longer periods are in no way harmful), were poured into a shallow petri dish and with the help of a fresh stock of fluid the ovarian tissues and membranes were removed very carefully. SIMPSON's method of cleaning the eggs by successive shakings in undiluted industrial alcohol and decanting, was found unnecessary. The only precaution to be taken is to see that the eggs do not come into contact with water once they have been immersed in GILSON's fluid. After cleaning, the eggs with the fluid were poured into a measuring jar and the exact volume recorded. This is an easy matter as all these eggs sink to the bottom of the jar. With the help of a small glass spoon of definite volume, $^1/_4$ ml. in this case, four aliquots were taken and the number of eggs in each were counted on a glass plate on which a number of squares are etched.

The female herrings under study were collected, along with mature males, a few weeks before the spawning period, which in the case of spring spawners of the western Baltic begins in April and for autumn spawners in October. Most of the ovaries were in maturity stages IV—V, which are ideally suited for such study. As has been observed by HICKLING (1940) the vast majority of eggs in the ovary of the herring ripen simultaneously and are spawned together. They are also approximately of equal size, as shown by FARRAN (1938). Very few of the eggs are small and evidently belong to the next spawning season. The latter, being lighter, remain at the top of the measuring jar and hence do not in any way affect the process of counting. Females in which the eggs had become glassy and transparent (stage VI) were not used, as they burst very easily when poured into GILSON's fluid.

Methods employed for calculating the relation between fecundity and length or weight

The mutual relationship between any two variables x and y can be expressed mathematically in the form of an equation, according to the function $y = f(x)$ where the form of the function f and its given constants $(a, b, \ldots)$ must be so selected as to result in the closest possible correlation between observed and calculated values. Which of the possible equations which can be derived from the functions $y = f(x)$ would best express the relationship, is determined partly from theoretical considerations, and partly, and even earlier, from the diagram of the observed values, and from the attempt to represent the relationship between y and x as a curve, or preferably a straight line. Regression equations of linear relationships can be easily calculated by means of the method of least squares; non-linear functions are chosen with a view to a change to a linear form by transformation of the variables.

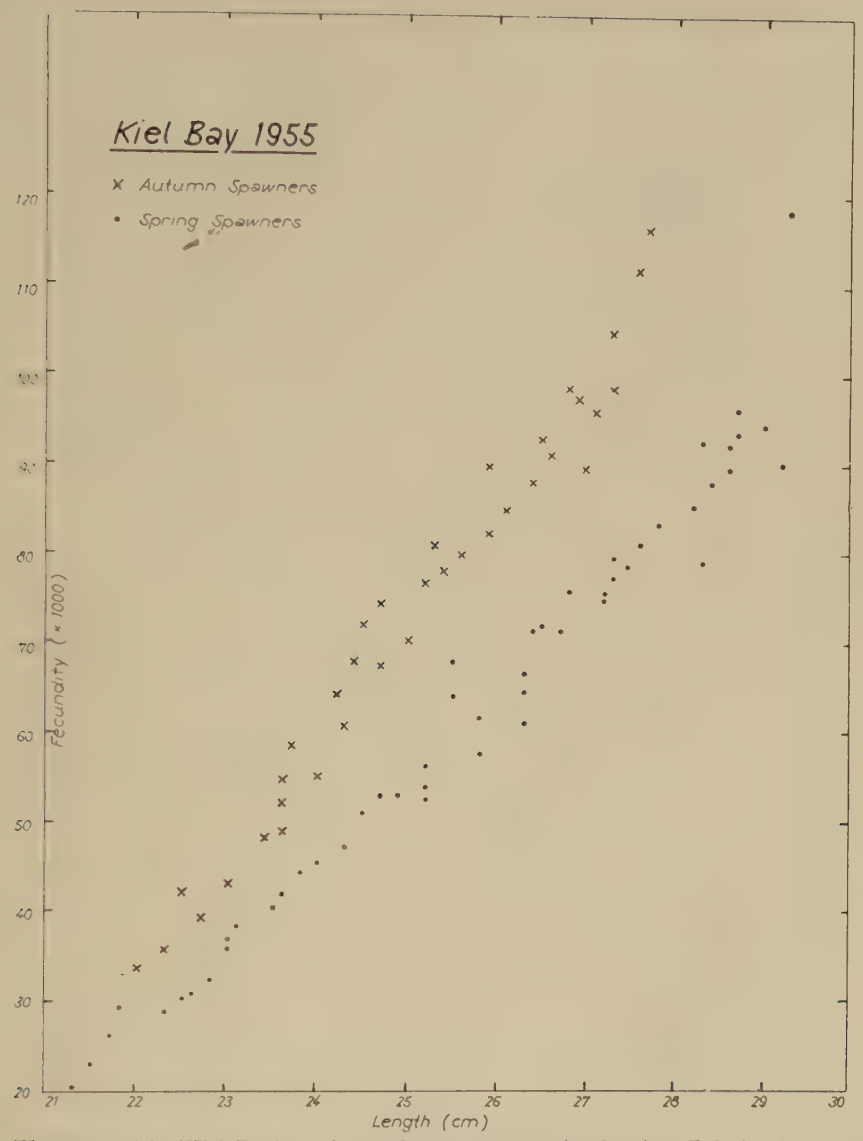


Figure 1. Western Baltic (Kiel Bay), spring and autumn spawning herring. Relation between fecundity and total length of the fish. Each dot and cross represents 1 fish.

In the present case, taking the observed fecundity and length or weight as the two variables y and x respectively, and plotting them as a scatter diagram (Fig. 1) it will be seen that in spite of the dispersal, there is a definite relation between the two. Depending on the functional relationship which we would like to show, various possibilities offer themselves for expressing this relationship as a mathematical equation. The distribution of the points in the diagram is such that the relation between fecundity (F) and length (L) can be expressed more or less approximately as a straight line or as a curve.

In the first instance, the linear relationship would be expressed by the formula:

$$F = f(L) = a + b \cdot L \tag{1}$$

In the second case, it would be an exponential relation:

$$F = f(L) = a \cdot L^b \tag{2}$$

by transformation into logarithms:

$$\log F = \log a + b \cdot \log L \tag{2a}$$

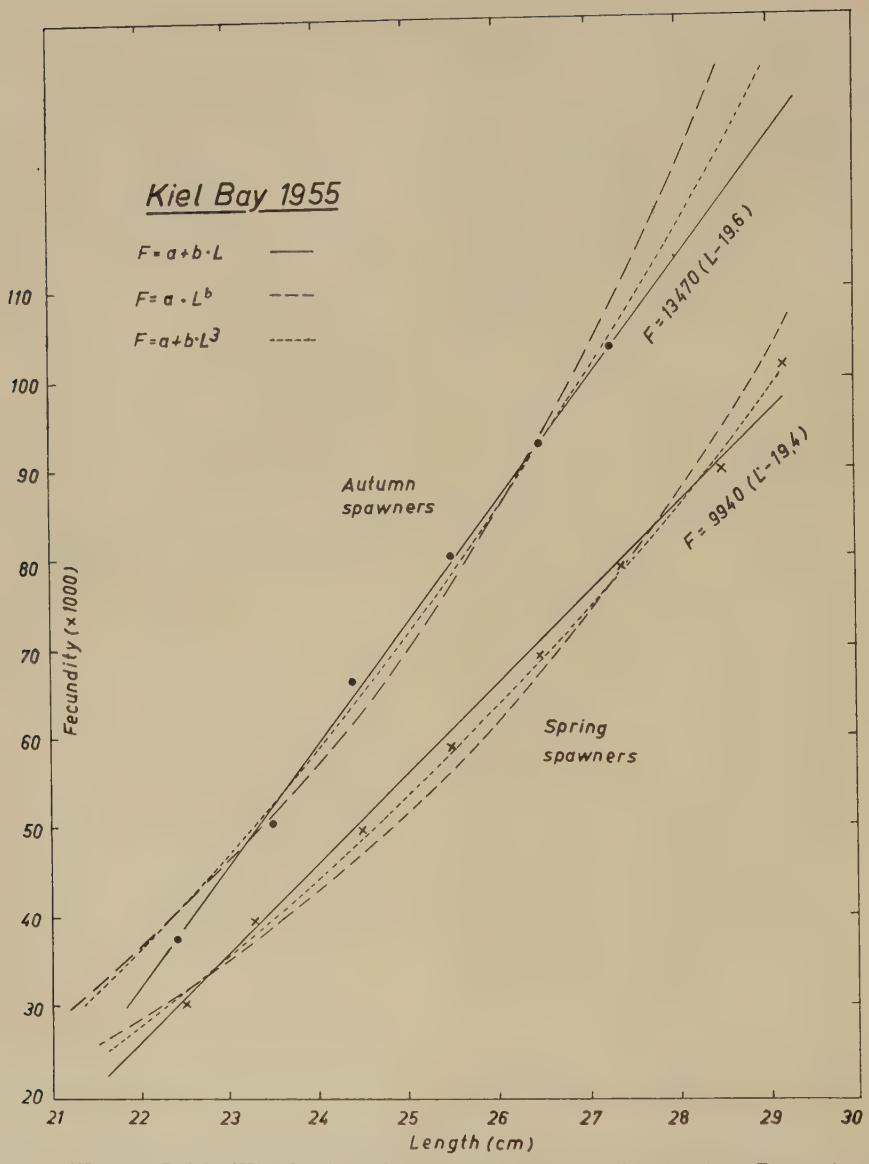


Figure 2. Western Baltic (Kiel Bay), spring and autumn spawning herring. Regression lines relating to fecundity and length.

It will further be shown, by graphical representation (Fig. 3), that there is a linear relation between fecundity and weight (W):

$$F = f(W) = a + b \cdot W \qquad (3)$$

In view of the fact that the weight (in g.) of a fish is proportional to the cube of length (in cm.): $W = \frac{k \cdot L^3}{100}$, it may therefore be assumed that in the same way, a linear relation exists between fecundity and the cube of length:

$$F = f(L^3) = a + b \cdot L^3 \qquad (4)$$

This is a special form of equation (2), assuming that $b = 3$, and inserting an additive constant. Applying the method of least squares to the empirical values, we obtain four different equations according to the above four formulae (1—4). We may accept, as giving the best expression of the relation between fecundity and length, the formula, which fulfils two conditions:

1. The calculated values should correspond as closely as possible to the observed values.
2. The equation should have a biological significance,

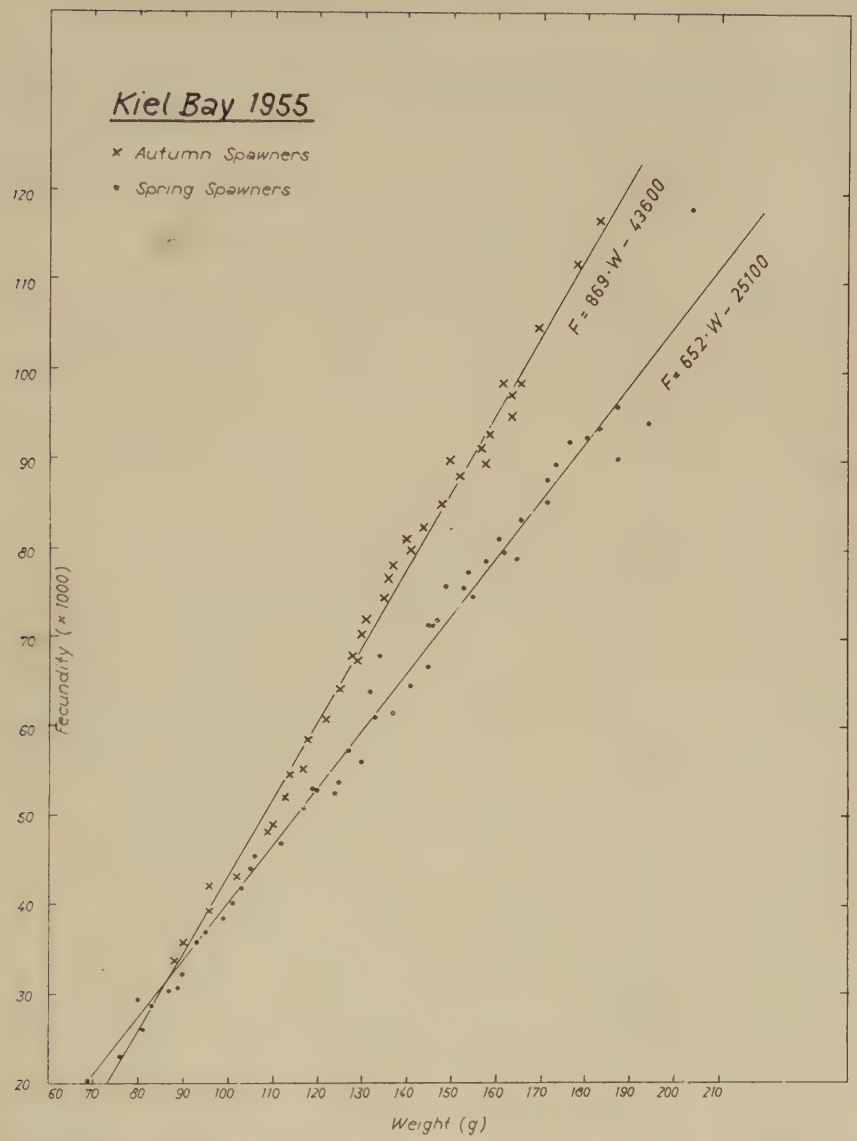


Figure 3. Western Baltic (Kiel Bay), spring and autumn spawning herring. Relation between fecundity and weight, single values and regression lines.

i.e., it should indicate the dependence of fecundity on length and at the same time give such values for the constants a and b as would serve for the comparison of different populations (races) or different species.

To test the validity of the four formulae used in determining the correlation between fecundity and length and weight respectively, the following values have been calculated from the observed and calculated numbers of eggs:—

1. Mean square of deviation:

$$\frac{(y_{obs.} - y_{calc.})^2}{n - 1}$$

2. Mean deviation, in %:

$$\pm \frac{100\, n \sqrt{\dfrac{\sum (y_{obs.} - y_{calc.})^2}{n - 1}}}{\sum (y_{calc.})}$$

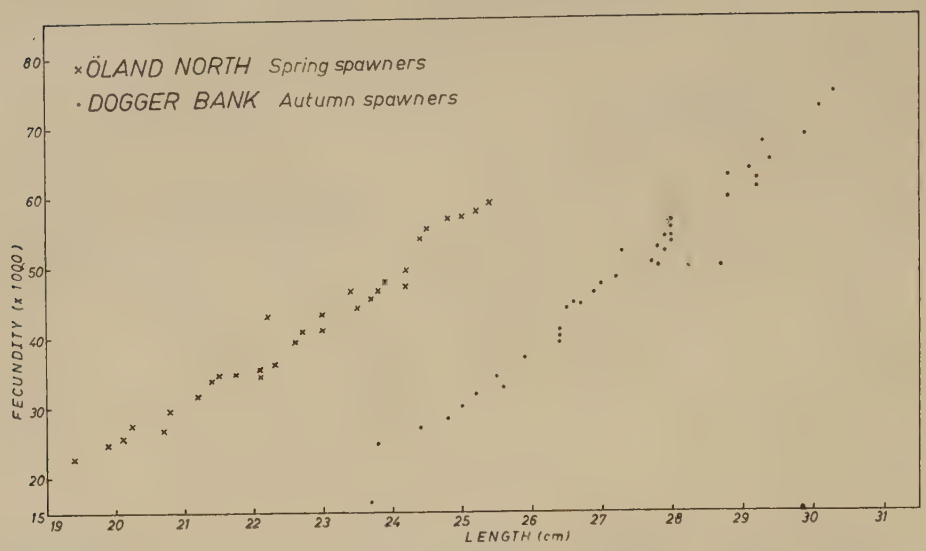


Figure 4. Central Baltic (Öland North), spring spawning herring, and North Sea (Dogger Bank), autumn spawning herring. Relation between fecundity and length of the fish. Each dot and cross represents 1 fish.

3. χ^2, i.e.: sum of the squares of deviation divided by calculated values:

$$\sum \frac{(y_{obs.} - y_{calc.})^2}{y_{calc.}}$$

The greater these values, the lesser is the validity of the formula used.

Simpson (1951) showed that there is a cubic relation between fecundity and length of the plaice. The values for F/L^3 and F/W although showing small fluctuations, were practically constant. This simple proportion between the number of eggs and the cube of length is a special form of equation (3) and (4), when a = almost nil.

Kändler and Pirwitz (1951) found in their studies on the fecundity of flatfish from the North Sea-Baltic area that this simple relationship is applicable only for plaice. In other species (flounder, dab) the value for a cannot be neglected.

In order to determine which of the three equations would give the best approximation for the correlation between fecundity and length, we have calculated our data using all three equations (1, 2, and 4), and also the equation for the correlation between fecundity and weight (3).

Results

The observations made on spring spawners from the western (51 ind.) and central Baltic (31 ind.), and on autumn spawners from western Baltic (36 ind.) and North Sea (40 ind.) are given in Figures 1, 3, 4, and 6 in the form of scatter diagrams. It will be seen at once that there is a close correlation between the fecundity and the length or weight of fish. Sometimes the number of eggs for any one size of fish vary between fairly wide limits. The values obtained for autumn spawners in Kiel Bay is always above the values for spring spawners from the same area, and the fecundity of herrings from the Dogger Bank is lower than that of fish of the same size from the Baltic.

To simplify the calculation, the material is divided into centimetre groups. Using the method of least squares we calculated the relation between fecundity and

1. total length: as a linear equation,
   as an exponential equation,
2. the cube of length, and
3. total weight

for each sample, from the average values of the centimetre groups (Table 1). As will be seen from the quotients F/L^3 and F/G, which show a distinct trend with increasing length and weight, a simple relationship between the number of eggs and length or weight does not exist. The equations obtained for the relation between fecundity and each of the three entities: total length (cm.), the cube of length, and total weight (g.) are given in Table 2. By means of these equations we calculated the number of eggs for each centimetre group from the average length and the average weight. These theoretical values will be found in Table 1 below the appertaining formula. The calculated values agree more or less with the observed mean numbers of eggs, as will be seen from the differences. Sometimes, the deviations show a special trend. In order to test the validity of the four equations used to study the relation between fecundity and length or weight as the case may be, we estimated

Table 1

Relation between fecundity (in 1000 eggs) and length resp. weight

Mean values for centimetre groups, observed and calculated, and differences between them

Frequency	Length range cm.	Average length cm.	Average weight g.	Mean No. of eggs × 1000	F/L	F/L^3	F/W	Calculated No. of eggs, $f(L)$	differences obs. — calc. Diff.	$f(L^3)$	Diff.	$f(L^3)$	Diff.	$f(W)$	Diff.
Western Baltic (Kiel Bay), autumn spawners															
4.....	22·0—·9	22·4	93	37·9	1·69	0·0036	0·41	37·8	0·1	40·1	—2·2	40·2	—2·3	37·2	0·7
6.....	23·0—·9	23·5	111	51·1	2·17	39	0·46	52·6	—1·5	51·1	0·0	52·5	—1·4	52·8	—1·7
7.....	24·0—·9	24·4	127	66·3	2·72	45	0·52	64·8	1·5	61·7	4·6	63·5	2·8	66·7	—0·4
7.....	25·0—·9	25·5	140	80·2	3·15	48	0·57	79·6	0·6	77·0	3·2	78·0	2·2	78·0	2·2
6.....	26·0—·9	26·5	157	92·7	3·50	49	0·59	93·0	—0·3	93·5	0·8	92·4	0·3	92·8	—0·1
6.....	27·0—·9	27·3	170	103·4	3·79	50	0·61	103·8	—0·4	108·8	—5·4	104·8	—1·4	104·1	—0·7
				Mean square of deviation					1·06		13·21		4·40		1·78
				Mean deviation %					±1·43		±5·04		±2·92		±1·85
				χ^2					0·085		0·871		0·374		0·137
Western Baltic (Kiel Bay), spring spawners															
4.....	21·0—·9	21·6	76	24·7	1·14	0·0025	0·33	22·2	2·5	26·4	—1·7	25·4	—0·7	24·6	0·1
4.....	22·0—·9	22·5	87	30·6	1·36	27	0·35	31·2	—0·6	31·8	—1·2	32·1	—1·5	31·7	—1·1
6.....	23·0—·9	23·3	99	39·7	1·70	31	0·40	39·2	0·5	37·4	2·3	38·5	1·2	39·5	0·2
5.....	24·0—·9	24·5	115	50·0	2·04	34	0·44	51·1	—1·1	47·1	2·9	49·0	1·0	50·0	0·0
7.....	25·0—·9	25·5	130	59·3	2·33	36	0·46	61·0	—1·7	56·6	2·7	58·5	0·8	59·8	—0·5
7.....	26·0—·9	26·5	143	69·3	2·62	37	0·49	71·0	—1·7	67·6	1·7	68·8	0·5	68·2	1·1
7.....	27·0—·9	27·4	158	79·1	2·89	38	0·50	79·9	—0·8	78·9	0·2	78·8	0·3	78·0	1·1
8.....	28·0—·9	28·5	176	90·0	3·16	39	0·51	90·8	—0·8	94·5	—4·5	91·5	—1·9	89·8	0·2
3.....	29·0—·9	29·2	196	101·5	3·48	41	0·52	97·8	3·7	105·8	—4·3	100·8	0·7	102·8	—1·3
				Mean square of deviation					3·60		8·37		1·28		0·71
				Mean deviation %					±3·14		±4·76		±1·87		±1·70
				χ^2					0·719		1·036		0·207		0·094
Central Baltic (Öland North), spring spawners															
2.....	19·0—·9	19·6	51·0	23·6	1·20	0·0031	0·47	22·3	1·3	23·9	—0·3	23·5	0·1	23·1	0·5
4.....	20·0—·9	20·5	59·5	27·4	1·34	32	0·46	27·9	—0·5	28·0	—0·6	27·9	—0·5	28·1	—0·7
4.....	21·0—·9	21·5	68·5	33·8	1·57	34	0·49	34·1	—0·3	33·2	0·6	33·4	0·4	33·4	0·4
6.....	22·0—·9	22·3	77·0	38·2	1·71	34	0·49	39·0	—0·8	37·7	0·5	38·1	0·1	38·4	—0·2
7.....	23·0—·9	23·5	89·0	45·0	1·92	35	0·51	46·4	—1·4	45·4	—0·4	45·8	—0·8	45·4	—0·4
5.....	24·0—·9	24·4	101·0	52·6	2·16	36	0·52	52·0	0·6	51·8	0·8	52·1	0·5	52·5	0·1
3.....	25·0—·9	25·2	110·0	58·0	2·30	36	0·53	57·0	1·0	58·1	—0·1	58·1	—0·1	57·8	0·2
				Mean square of deviation					1·00		0·31		0·22		0·19
				Mean deviation %					±2·51		±1·40		±1·18		±1·10
				χ^2					0·852		0·050		0·034		0·038
North Sea (Dogger Bank), autumn spawners															
2.....	23·0—·9	23·7	115	20·7	0·87	0·0016	0·18	20·5	0·2	22·6	—1·9	21·8	—1·1	18·3	2·4
2.....	24·0—·9	24·6	140	27·7	1·13	19	0·20	27·6	0·1	27·3	0·4	27·6	0·1	27·9	—0·2
5.....	25·0—·9	25·4	156	33·2	1·31	20	0·21	33·9	—0·7	32·0	1·2	33·0	0·2	34·0	—0·8
8.....	26·0—·9	26·6	179	42·9	1·61	23	0·24	43·3	—0·4	40·5	2·4	41·9	1·0	42·8	0·1
8.....	27·0—·9	27·6	200	50·8	1·84	24	0·25	51·2	—0·4	48·8	2·0	50·0	0·8	50·9	—0·1
7.....	28·0—·9	28·3	212	55·9	1·98	25	0·26	56·6	—0·7	55·4	0·5	55·9	0·0	55·9	0·0
6.....	29·0—·9	29·3	241	64·5	2·20	26	0·27	64·5	0·0	66·1	—1·6	65·0	—0·5	66·5	—2·0
2.....	30·0—·9	30·2	256	73·3	2·43	27	0·29	71·6	1·7	77·0	—3·7	73·7	—0·4	72·4	0·9
				Mean square of deviation					0·61		4·50		0·47		1·62
				Mean deviation %					±1·69		±4·59		±1·49		±2·76
				χ^2					0·073		0·656		0·100		0·407

Table 2
Regression equations relating to fecundity and length resp. weight

Area and race	Relation between fecundity and total length $F = a + b \cdot L$	total length $F = a \cdot L^b$	cube of length $F = a + b \cdot L^3$	total weight $F = a + b \cdot W$
Western Baltic (Kiel Bay) autumn spawners	$y = -263{\cdot}9 + 13{\cdot}469 \cdot x$ $F = 13470\ (L - 19{\cdot}6)$	$y = -5{\cdot}209 + 5{\cdot}045 \cdot x$ $F = 0{\cdot}006186 \cdot L^{5{\cdot}045}$	$y = -39{\cdot}486 + 0{\cdot}00709 \cdot x$ $F = 7{\cdot}09 \cdot L^3 - 39500$	$y = -43{\cdot}64 + 0{\cdot}869 \cdot x$ $F = 869 \cdot W - 43600$
Western Baltic (Kiel Bay) spring spawners	$y = -192{\cdot}5 + 9{\cdot}942 \cdot x$ $F = 9940\ (L - 19{\cdot}4)$	$y = -4{\cdot}729 + 4{\cdot}609 \cdot x$ $F = 0{\cdot}01866 \cdot L^{4{\cdot}609}$	$y = -25{\cdot}855 + 0{\cdot}00509 \cdot x$ $F = 5{\cdot}09 \cdot L^3 - 25900$	$y = -25{\cdot}07 + 0{\cdot}652 \cdot x$ $F = 652 \cdot W - 25100$
Central Baltic (Öland North) spring spawners	$y = -99{\cdot}1 + 6{\cdot}192 \cdot x$ $F = 6190\ (L - 16{\cdot}0)$	$y = -3{\cdot}183 + 3{\cdot}531 \cdot x$ $F = 0{\cdot}6561 \cdot L^{3{\cdot}531}$	$y = -7{\cdot}300 + 0{\cdot}00409 \cdot x$ $F = 4{\cdot}09 \cdot L^3 - 7300$	$y = -6{\cdot}90 + 0{\cdot}588 \cdot x$ $F = 588 \cdot W - 6900$
North Sea (Dogger Bank) autumn spawners	$y = -1{\cdot}65 + 7{\cdot}850 \cdot x$ $F = 7850\ (L - 21{\cdot}1)$	$y = -5{\cdot}607 + 5{\cdot}063 \cdot x$ $F = 0{\cdot}002472 \cdot L^{5{\cdot}063}$	$y = -26{\cdot}721 + 0{\cdot}00365 \cdot x$ $F = 3{\cdot}65 \cdot L^3 - 26700$	$y = -25{\cdot}93 + 0{\cdot}384 \cdot x$ $F = 384 \cdot W - 25900$
Southern North Sea[1] (East Anglia) autumn spawners	$y = -54{\cdot}772 + 3{\cdot}050 \cdot x$ $F = 3050\ (L - 18{\cdot}0)$	$y = -0{\cdot}530 + 3{\cdot}465 \cdot x$ $F = 0{\cdot}2954 \cdot L^{3{\cdot}465}$	$y = -2{\cdot}460 + 0{\cdot}00149 \cdot x$ $F = 1{\cdot}49 \cdot L^3 - 2460$	

[1]) Calculated from data given by HICKLING (1940).

the mean square of deviation, the mean deviation in %, and the value of χ^2. The results obtained are given in Table 1.

We see that the linear equation between fecundity and total weight gives the nearest approximate values for the number of eggs, except the autumn spawners of Dogger Bank. Very good results are obtained in all four samples by the linear equation relating to fecundity and the cube of length. This was to be expected because the weight is proportional to the cube of length. In all samples except that from the central Baltic, there is a comparatively greater deviation between observed and calculated values obtained by the exponential equation for the relation between fecundity and total length, than by the other equations. It is very remarkable that the linear equation between fecundity and length in all cases except one, will bring observed values more in accord with calculated values, than the exponential function.

Obviously, the regression equation of the formula $y = a + bx$ is more suitable for expressing the relation between the number of eggs and the size of fish, than the function $y = ax^b$. The production of eggs does not begin until the fish has reached a certain size, at which it becomes fertile. We may assume that from this minimum size when the number of eggs is nil, the fecundity increases with size in a linear or exponential relation. From the regression equation $y = a + bx$, we obtain the quotient a/b which represents the theoretical size of fish at its first maturity. The nearest approximation to this value is obtained by the linear equation beween fecundity and length, as is seen from Figures 2 and 5. The theoretical size at which maturity can be reached (Table 2), is lowest in the central Baltic (16·0 cm.) highest in the North Sea, Dogger Bank (21·1 cm.); the values are intermediate in the western Baltic (19·4—19·6 cm.).

From the linear equations, especially from the regression coefficient b, we can derive the rate of increase in fecundity with growth in length and weight, for the different races of herrings:—

Area	Number of eggs for every 1 cm.	Number of eggs for every 10 g.
Western Baltic (Kiel Bay), autumn spawners	13,470	8,690
Western Baltic (Kiel Bay), spring spawners	9,940	6,520
Central Baltic (Öland North), spring spawners	6,190	5,880
North Sea (Dogger Bank), autumn spawners	7,850	3,840
Southern North Sea (East Anglia), autumn spawners	3,050	

The minimum rate of increase in fecundity with growth in length is observed in the East Anglian herring, followed by that of the Dogger Bank. It is still higher in herring from the western Baltic, especially in autumn spawners. A decrease is again noticeable in herring from the central Baltic. The rate of increase in fecundity with growth in weight follows a similar pattern, being lowest in herring from the Dogger Bank (probably still lower in East Anglian herring), and highest in the autumn spawners of Kiel Bay. In herring from the central Baltic it is perceptibly higher than in those from the Dogger Bank, in contrast to the relation with increasing length. This difference is caused by the very low length-weight coefficient of herring from the central Baltic (0·69), which amounts to 0·77 and 0·84 respectively in herring from the western Baltic, and to 0·94 in the North Sea.

The exponential equation $F = a \cdot L^b$ is not very instructive for purposes of the comparison of different populations, as the regression coefficients do not vary

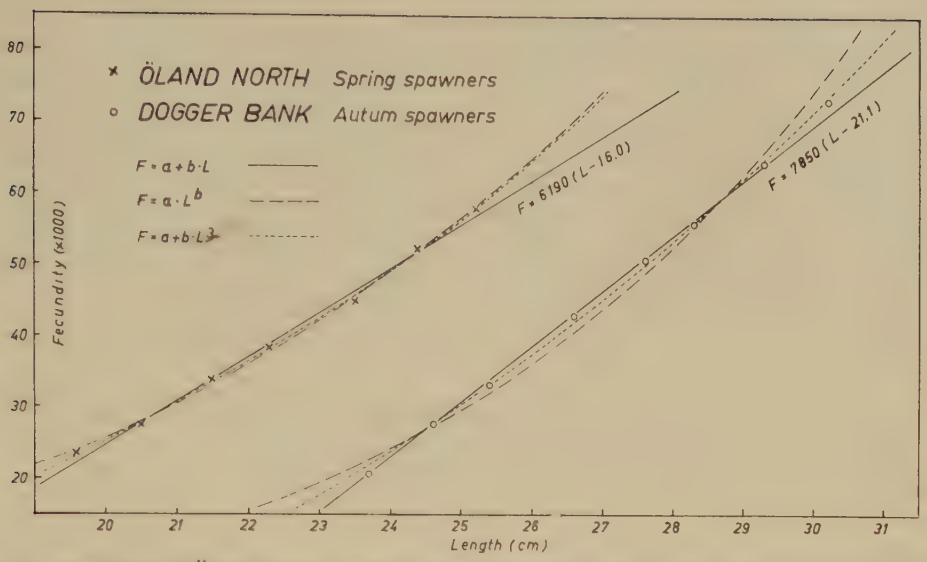


Figure 5. Central Baltic (Öland North), spring spawning herring, and North Sea (Dogger Bank), autumn spawning herring. Regression lines relating to fecundity and length.

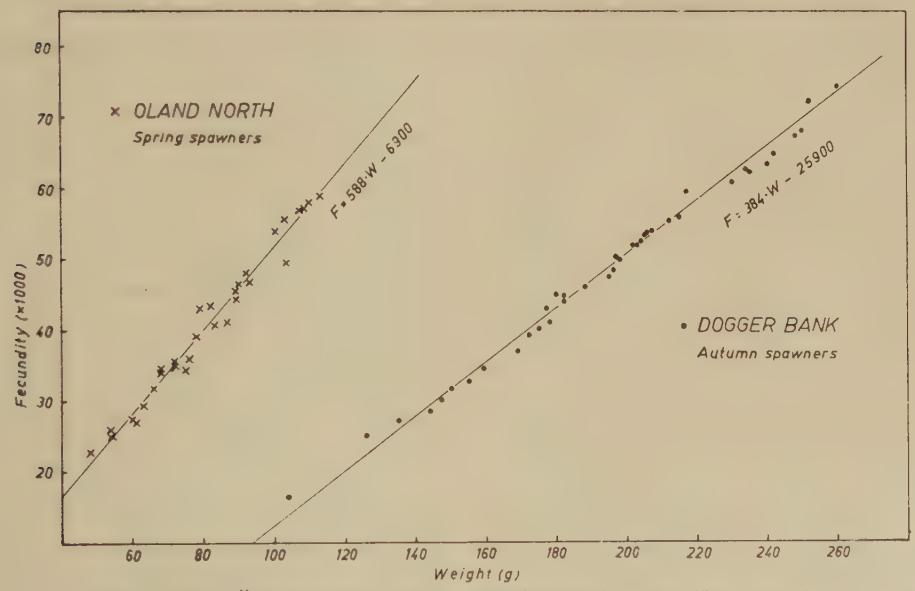


Figure 6. Central Baltic (Öland North), spring spawning herring, and North Sea (Dogger Bank), autumn spawning herring. Relation between fecundity and weight, single values and regression lines.

independently from each other, and within fairly wide limits, b between 3·47 and 5·06, a between 0·3 and 0·0025. The ovaries do not form a constant proportion of the fish with increasing weight (and hence with length). In all the four races of herring examined, the gonads become, with growth, an increasingly greater burden for the fish and this is in conformity with the observation that the rate of increase of fecundity is higher than the cube of length, if an equation is used without an additive

factor. The higher the exponent b, the more rapidly the weight of the ovary will increase in relation to the total weight of fish. In herring from the Dogger Bank and the western Baltic, it rises from 12—13% to 22—23% of body weight. On the other hand, the regression coefficient a depends on the size of the exponent b: the larger b, the smaller is a.

This study is a first attempt to make a comparison between the fecundity of the different herring populations. Although the mathematical treatment of the material may be perfected, yet the results demonstrate that the estimation of the fecundity offers some new aspects in racial investigations.

References

Dutt, S., 1956. "On the fecundity of Baltic herrings, the growth and racial characters of the juveniles of spring and autumn spawners of Kiel Bay". Dissertation Kiel.

Farran, G. P., 1938. "On the size and number of the ova of Irish herring". J. du Cons., **13** (2).

Hickling, G. F., 1940. "The fecundity of the herring of the Southern North Sea". Journ. Mar. Biol. Assoc., **24**.

Jenkins, J. T., 1902. "Altersbestimmung durch Otolithen bei den Clupeiden". Wiss. Meeresunters., Abt. Kiel, **6**.

Kändler, R., & Pirwitz, W., 1957. "Über die Fruchtbarkeit der Plattfische im Nordsee-Ostsee-Raum". Kieler Meeresf., **13**.

Simpson, A. G. (1951): "The fecundity of the plaice". Fish. Invest., Ser. 2, **17** (5).

14.

Number of Pectoral Fin Rays in the Spring and Autumn Spawning Herring in Kiel Bay

By S. Dutt

The spring and autumn spawning herring of the western Baltic have been the subject of study for a fairly long time. But although it has been shown by several authors that the two races have some distinctive characteristics, it has not been an easy matter until now to identify individuals of the two races when occurring together, except during the spawning time, and it has been especially difficult in the case of juveniles. The number of prehaemal vertebrae has been shown so far to be the only character that can be completely relied upon, but the determination of this character involves the examination of large samples, and extreme care, and hence, considerable time. I have attempted to establish a reliable and time-saving method of identification especially of the juveniles of the two races in relatively small samples, from one of the external characters, viz., by determining the number of pectoral fin rays.

Very little attention has been paid to the number of pectoral fin rays in the racial studies of herring, although E. Ehrenbaum holds the view that it is one of the characters which must be considered in detail in such studies. Although no racial study would be complete without taking into account the vertebral number, the number of pectoral fin rays must also be considered in detail, especially in comparing two races from the same area, and particularly herring from the western Baltic, where the difference in the vertebral number of spring and autumn spawners is very small. The autumn spawners generally have a slightly higher vertebral number than spring spawners, but it may happen that in a random sample in which the two races occur together, we get a higher value for the spring spawners than for the autumn spawners. In such cases, while the number of prehaemal vertebrae no doubt gives a clue to the race, confirmation can be obtained by determining the number of pectoral fin rays.

In view of the above facts, the determination of the number of the pectoral fin rays in juvenile herring from Kiel Bay was begun. The samples were taken from herring landed at the Kiel fish market during the period July 1954—January 1956. In many of the samples, juveniles of the two races were mixed and it was not possible to distinguish them from their length only. The method employed for the purpose was as follows: after the juvenile herring had been sorted into centimetre groups and weighed, the left pectoral fin was carefully removed, cleaned and preserved in 4% formalin for 2—3 hours. It was then washed in tap water for about half an hour to remove the excessive formalin, and stained for about three hours in a solution of alizarin in 70% alcohol. At the end of this period the fin rays were thoroughly stained and could be counted very easily under a microscope. In about 10% of the fins examined, one or rarely two rays were either smaller in size or rudimentary. These however were counted as fully developed rays. Care was taken to see that only the fins from the left side were used throughout the study. By employing this method it was possible to determine the number of fin rays (and hence the race) within a few hours after the landing of the fish.

Table 1 gives the results obtained from the centimetre groups, representing juvenile spring and autumn spawners respectively.

In 1822 juvenile spring spawners belonging to the 1954 and 1955 year-classes, the mean number of rays in the left pectoral fin is 16·91 $\pm$ 0·020. The averages for the two year-classes are practically the same: 16·91 and 16·89 respectively. The mean values of the 10 samples vary between 16·55 $\pm$ 0·071 and 17·10 $\pm$ 0·127, showing a difference of 0·55 $\pm$ 0·145, which is significant.

In 2196 juvenile autumn spawners the mean number of rays in the left pectoral fin is 18·32 $\pm$

Table 1
Number of rays in the left pectoral fin of juvenile herring in Kiel Bay

a) Spring spawners

Date		Length cm.	14	15	16	17	18	19	20	n	M	σ	σ_M	Year-class
July	1954	4— 5	1	6	42	87	41	5	1	183	16·98	± 0·892	± 0·066	1954
August	1954	4— 7	—	21	129	303	143	17	5	618	17·03	± 0·871	± 0·035	1954
Oct.	1954	8—10	—	7	41	90	33	4	2	177	16·95	± 0·878	± 0·066	1954
Dec.	1954	8—13	—	12	95	158	47	8	1	321	16·83	± 0·834	± 0·047	1954
Jan.	1955	10—11	—	3	49	83	29	4	—	168	16·89	± 0·790	± 0·061	1954
June	1955	10—12	—	4	45	43	18	—	—	110	16·68	± 0·790	± 0·076	1954
July	1955	10—16	—	7	56	44	15	—	—	122	16·55	± 0·784	± 0·071	1954
Total		4—16	1	60	457	808	326	38	9	1699	16·91	± 0·859	± 0·021	1954
Oct.	1955	4— 6	—	3	25	22	9	2	—	61	16·70	± 0·902	± 0·115	1955
Nov.	1955	7— 8	—	1	4	9	5	1	—	20	17·05	± 0·945	± 0·211	1955
Jan.	1956	8— 9	—	—	10	20	10	2	—	42	17·10	± 0·821	± 0·127	1955
Total		4— 9	—	4	39	51	24	5	—	123	16·89	± 0·895	± 0·081	1955
Grand total			1	64	496	859	350	43	9	1822	16·91	± 0·860	± 0·020	1954/55

b) Autumn spawners

Date		Length, cm.	15	16	17	18	19	20	21	n	M	σ	σ_M	Year-class
July	1954	7— 9	—	7	29	90	71	15	2	214	18·30	± 0·937	± 0·064	1953
August	1954	8—10	—	8	83	236	134	41	—	502	18·23	± 0·878	± 0·039	1953
Oct.	1954	11	—	1	4	9	5	2	—	21	18·14	± 1·015	± 0·221	1953
Dec.	1954	14—17	—	1	7	28	23	4	—	63	18·35	± 0·827	± 0·104	1953
Total			—	17	123	363	233	62	2	800	18·26	± 0·893	± 0·032	1953
July	1955	5— 9	—	9	61	199	165	57	4	495	18·43	± 0·939	± 0·042	1954
Sept.	1955	7—10	—	6	26	71	47	26	1	177	18·36	± 1·031	± 0·077	1954
Oct.	1955	7—15	2	21	84	222	159	67	6	561	18·32	± 1·044	± 0·044	1954
Nov.	1955	9—13	—	2	12	19	14	6	—	53	18·20	± 1·039	± 0·143	1954
Jan.	1956	11—12	—	7	23	36	29	13	2	110	18·22	± 1·153	± 0·110	1954
Total			2	45	206	547	414	169	13	1396	18·35	± 1·016	± 0·027	1954
Grand Total			2	62	329	910	647	231	15	2196	18·32	± 0·974	± 0·021	1953/54

0·021. The averages for the two year-classes investigated, 1953 and 1954, are only slightly different, 18·26 and 18·35 respectively, and the difference between the two: 0·09 ± 0·042 is not significant. The means of the 9 samples vary but slightly, between 18·14 ± 0·221 and 18·43 ± 0·042, showing a difference of only 0·29 ± 0·22, which is not significant.

From Table 1, we observe that between the sample of spring spawners with the highest mean number of pectoral fin rays (17·10 ± 0·127) and the sample of autumn spawners with the lowest mean number (18·14 ± 0·221), there is a difference of 1·04 ± 0·256. The mean difference of the two small samples (42 and 21 ind.) is more than four times the standard error of difference.

Comparing the mean number of rays in the left pectoral fin of herring from the western Baltic, we obtain the following figures:—

	n	M	σ_M
Juvenile spring spawners	1822	16·91	± 0·020
Juvenile autumn spawners	2196	18·32	± 0·021
Difference...		1·41	± 0·029

The pectoral fin rays were similarly counted in three samples of adult herring from the Kiel Bay, partly used for estimating the fecundity. The values obtained for these are given in Table 2.

The value of 17·31 ± 0·048 obtained for the spring spawners agrees very well with the value of 17·25 ± 0·075 obtained for 93 adult herring in 1946 (KÄNDLER, unpublished). It is interesting to note that the average values obtained for the adults are slightly different from those obtained for juveniles, as they approach one another (cf. the frequency curves in Fig. 1). The difference between the two races is only 0·71 ± 0·134 for adults, i.e., half of that of juveniles.

Table 2

Number of rays in the left pectoral fin of adult spring and autumn spawning herring in Kiel Bay

	15	16	17	18	19	20	21	n	M	σ	σ_M
Spring spawners	2	19	130	71	12	—	—	234	17.31	± 0.730	± 0.048
Autumn spawners	—	1	14	24	12	1	1	53	18.02	± 0.909	± 0.125
								Difference		0.71	± 0.134

Table 3

Number of rays in the left pectoral fin of juvenile herring from the samples studied for estimating the growth-rate

Date	Length, cm.	n	M	15	16	17	18	19	20	21	Race
				a) July 1954—January 1955							
23- 7-1954	4—5	66	16·91	3	14	36	12	1	—	—	Spring
	6	23	17·26	—	6	10	4	1	2	—	Mixed
	7—9	104	18·28	—	3	15	47	28	11	—	Autumn
19- 8-1954	6	38	16·95	1	10	18	8	1	—	—	Spring
	7	123	17·17	5	22	56	31	5	4	—	Mixed
	8—10	388	17·96	1	22	106	152	82	21	4	Autumn
20- 8-1954	4—6	457	17·00	15	97	229	104	11	1	—	Spring
25- 8-1954	8—10	217	18·29	—	3	33	100	61	20	—	Autumn
22-10-1954	8—10	177	16·95	7	41	90	33	4	2	—	Spring
	11—13	23	18·17	—	1	4	10	6	2	—	Autumn
16-12-1954	8—9	123	16·85	6	34	59	21	3	—	—	Spring
	11—12	58	16·64	5	18	28	7	—	—	—	Spring
18-12-1954	11—12	90	16·82	—	32	47	7	3	1	—	Spring
	13—14	32	17·63	—	7	11	6	4	3	1	Mixed
11- 1-1955	10—12	103	16·84	2	32	52	15	2	—	—	Spring
	13—14	34	17·50	1	5	9	14	5	—	—	Mixed
				b) June 1955—January 1956							
18- 6-1955	10—12	110	16·68	4	45	43	18	—	—	—	Spring
15- 7-1955	9	7	18·14	—	—	1	4	2	—	—	Autumn
	12—16	105	16·55	6	48	38	13	—	—	—	Spring
20/21-7-55	5—9	495	18·43	—	9	61	199	165	57	4	Autumn
	10—16	17	16·53	1	8	6	2	—	—	—	Spring
28- 9-1955	7—10	177	18·36	—	6	26	71	47	26	1	Autumn
3-10-1955	8·5—9·0	72	17·74	—	14	19	19	12	8	—	Mixed
	9·5—14	143	18·21	—	8	21	62	37	15	—	Autumn
12-10-1955	9—12	97	18·45	—	5	10	36	30	14	2	Autumn
30-11-1955	7—8	20	17·05	1	4	9	5	1	—	—	Spring
	9·0	21	17·38	—	5	7	6	2	1	—	Mixed
	9·5—13	53	18·19	—	2	12	19	14	6	—	Autumn
3- 1-1956	8—9·0	42	17·10	—	10	20	10	2	—	—	Spring
	9·5/11—14	172	18·18	—	10	35	63	43	20	1	Autumn

From this it is clear that there is a very distinct difference in the number of pectoral fin rays of spring and autumn spawners from the western Baltic. They therefore form an external character of considerable importance in racial studies. From the number of pectoral fin rays, the race can be determined without difficulty, in a relatively short time and, what is more important, with a great amount of certainty even in small samples, as will be seen from Table 1.

As mentioned, the number of pectoral fin rays was used to distinguish the two races of juvenile herring in Kiel Bay. Samples from the catches landed at Kiel fish market were studied with a view to determining the size composition and, from the shifting of the maxima in the length distribution, to observe the growth-rate of descendents of spring and autumn spawners (Table 3).

During the period July 1954—January 1955, a series of 18 samples were examined. The fish were sorted into centimetre groups (all the fish from x·0—x·9 cm. being included under the x cm. group), the number of fish in each group was counted, weighed, and the number of rays in the left pectoral fin determined.

The values for 9 of the most important samples are shown in a percentage frequency curve in Figure 2. The frequency curve for the first sample (23. July 1954) shows two distinct maxima: at 4 cm. and 8 cm. respectively (this sample was caught with a small narrow-meshed seine in the Kiel harbour). As the year advances, these two maxima also advance, but the difference between them diminishes. In January 1955, the maxima lie at 10 cm. and 13 cm. respectively, and the difference is reduced to 3 cm. Of course, the length distribution in the samples depends on the

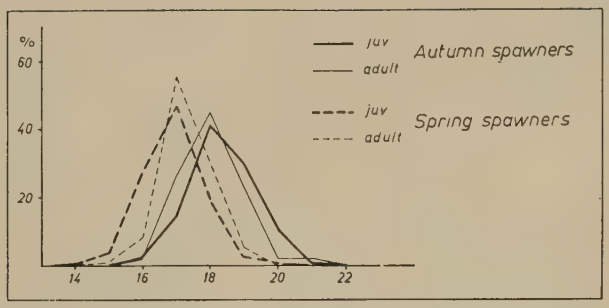


Figure 1. Percentage frequency of pectoral fin rays (left side) in juvenile and adult herrings of Kiel Bay (western Baltic).

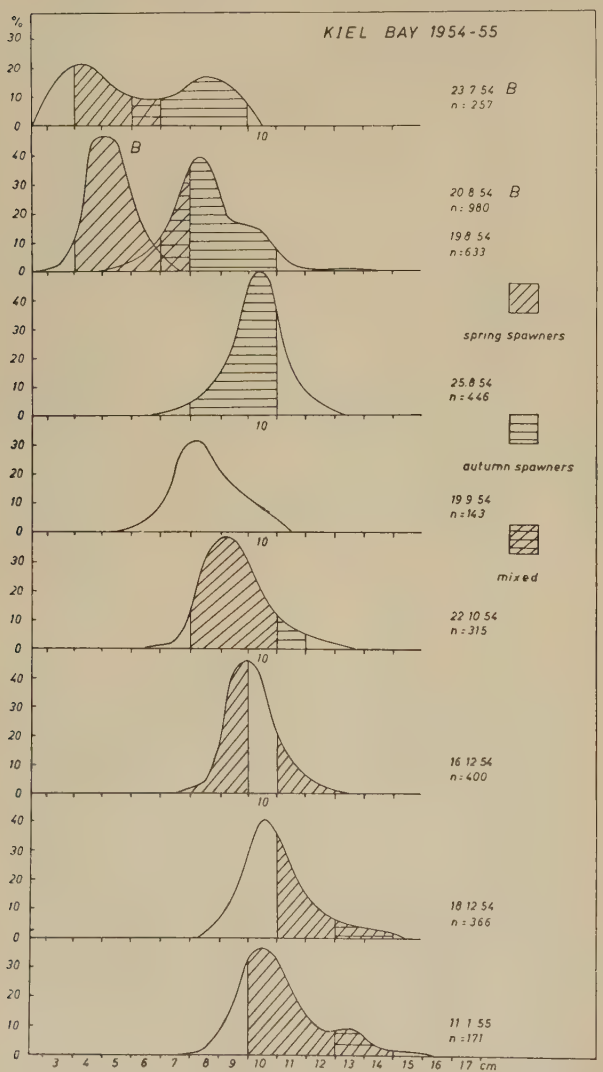


Figure 2. Length distribution of juvenile herring, caught off the Kiel Fjord from July 1954 to January 1955.

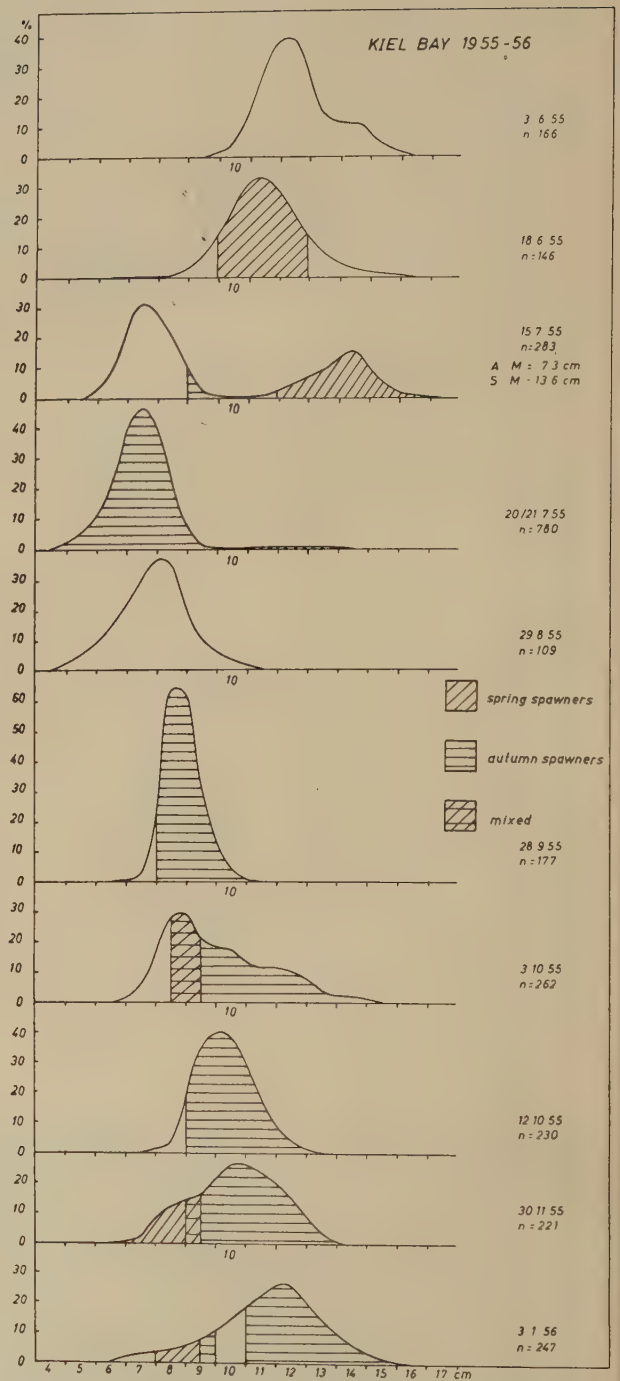


Figure 3. Length distribution of juvenile herring, caught off the Kiel Fjord from June 1955 to January 1956.

place of capture and the type of gear used. The count of the number of pectoral fin rays (Table 3) shows that the first maximum moving from 4 cm. in July to 10 cm. in January 1955 belongs to the juveniles of spring spawners in the first year of life (1954 year-class), whereas the second maximum rising from 8 cm. in July 1954 to 13 cm. in January 1955 belongs to the juveniles of autumn spawners at the end of their first and the beginning of their second year of life (1953 year-class).

The sample taken on 20. August 1954 in the Kiel harbour is composed only of young spring spawners, and that of 25. August 1954 contains only juveniles of autumn spawners. The sample taken on 19. August 1954 is composed chiefly of young autumn spawners, and a few spring spawners. In all the other samples the two races are mixed, and the juveniles of spring spawners almost always predominate over those of autumn spawners. In the samples of 18. December 1954 and 11. January 1955 the juvenile autumn spawners are surpassed in numbers by those of spring spawners.

The rate of growth from July 1954 to January 1955 established in this way is 6 cm. for spring spawners and 4—5 cm. for autumn spawners. It is clearly seen that the juveniles of spring spawners gradually outnumber those of autumn spawners from month to month, as they grow up.

The investigations on the juvenile herring were continued the next year, from June 1955 to January 1956 (Fig. 3). These observations present in many ways a very different picture from that of the year 1954. The two samples taken in June 1955 from catches with the trawl consist mainly of one-year-old spring spawners of the 1954 year-class. These herring which were about 10 cm. in January have reached an average length of 13·6 cm. by the middle of July as is demonstrated by the sample from 15. July 1955. In this sample there is a mixture of the two races, and it is the abundant 1954 year-class (of *autumn spawners*) which now appears in large numbers, and dominates in the samples in the following months. In this regard, the catches of this year differ markedly from those of the previous year in which the juveniles of *spring spawners* dominated.

There is another remarkable difference between the two years. The predominant juveniles of autumn spawners in 1955 (1954 year-class) are much smaller in size in comparison with those of the previous year (1953 year-class). Thus, for example, on 15. July 1955 they average 7·3 cm. in length and on 28. September 1955 they average 8·4 cm., whereas in the previous year they had already reached a length of 9·7 cm. on 25. August 1954. It is only in the samples from the end of the year 1955 that there is an indication of a sudden growth of individuals of the 1954 year-class, but even then the average length is about 11—12 cm., which is about 2 cm. less than the mean length of the previous year-class at the same age.

Juveniles of spring spawners form only a small proportion of the samples, and this year-class also shows a slower growth than the previous year-class. In January 1956 they have reached a length of only 8—9 cm., whereas in the previous year they had reached a length of 10—11 cm. This retarded growth of juveniles of spring spawners is evident in a sample taken on 5. October 1955 in Kiel harbour. This catch was composed mostly of young sprats of about 4 cm. length (95 %), but it included a sprinkling of juveniles of spring and autumn spawners. The spring spawners had an average length of only 4·8 cm.

The explanation of the differences in the growth of juvenile herring in Kiel Bay and especially in the Kiel Fjord must be ascribed to the unusual weather in the summer of 1954 and 1955.

The summer of 1954 in northern Germany was exceptionally cold. After a very cold, late winter with water temperatures near 0° C. in Kiel Fjord in February and March, the monthly mean temperature rose steadily to 15° in June and it remained at this low level until September, when it dropped again. In contrast to this, the summer of 1955 was unusually warm. After a very cold, late winter as in 1954, and a cool spring, the mean water temperature rose to 18° in July and to 20° in August. A maximum of 21·9° was observed on 16. July 1955. In autumn the water temperature was normal.

The fact that the growth of young herring was slow in the warm summer of 1955 may be attributed to the injurious influence of high water temperatures on the herring, which as a boreal fish is accustomed to colder waters and avoids too warm waters. In the coastal waters and in the narrow fjords it could not escape the warm waters, and in some places feeble and dying, or dead young herring were observed floating on the surface and falling an easy prey to the gulls. Perhaps lack of food was an additional cause of their mortality. The high water temperatures in the summer of 1955 were caused by constant high barometric pressure over northern Europe, accompanied by easterly winds which carried the Baltic water of low salinity westward, so that it formed the upper layer also, in Kiel Bay. This Baltic surface water proved to be very poor in food (copepods) for herring.

On the other hand, the mean surface salinity in the summer of 1954 (July to September) was exceptionally high, as a result of the westerly winds which carried the surface water of low salinity in the western Baltic eastwards and caused the deeper waters of higher salinity in the coastal area to ascend. Probably the lower water temperatures and the higher salinity in the summer and autumn of 1954 were also the cause of the abundance of the autumn-spawning 1954 year-class.

15.

Differentiation of the Biological Groups of Herring in the Southern Baltic

By Józef Popiel

1. Introduction

The herring living in the Baltic differ considerably from the North Sea herring. This has already been established by F. Heincke (6), F. K. Suworow (14), G. Schneider (12), and others. These herring are even given different names in the different countries, such as "strömming" or "salaka", which underlines the peculiarities of these fish. In spite of this fact it is difficult to distinguish the Baltic herring from the herring which occur in the Belts and Sound. The latter have many features in common with the North Sea stocks.

It is recognized that the limit to which the typical small Baltic herring reach is the line connecting the Isle of Öland with Gdansk Bay. The herring which occur to the west of this border line are considered to be closely related to the Belt and Sound herring.

It appears clearly from the investigations of L. A. Rannak (11) and N. N. Spaski (13), carried out in recent years in the eastern part of the Baltic, that the occurrence of the typical, small, slow-growing herring is confined to the Gulf of Finland and Riga Bay. This herring differ considerably from the herring caught in the Klajpeda region and Gdansk Bay. The herring occurring off the western coast of the Baltic was described in detail by Hessle (7). It will be referred to below.

2. The spring and autumn herring

The presence of these two groups in Gdansk Bay has already been stated by K. Demel (3).

We are able to distinguish between the adult spring and autumn herring on the basis of differences in the maturation cycle, such as has been described by W. Cieglewicz and K. Posadzki (2).

The differences which are due to the two spawning periods appear from the structure of the otoliths (R. Kändler (8); H. Einarsson (4); J. Popiel (10)). This fact affords an additional possibility of recognizing the herring, this being particularly indispensable in the case of immature fish.

The percentage of autumn-spawning herring decreased considerably in the period 1946—1951 as a result of the absence of young and abundant year-classes, the catches being predominated by old, large herring, probably belonging to the 1937 year-class.

During recent years changes have taken place. There was the fairly good 1948 year-class and at present a still more numerous brood from the autumn of 1952. At the same time, the percentage of autumn herring in the catches has increased considerably, as compared with the spring spawners. These changes are more apparent in the Bornholm Basin than in the Gdansk Bay. The autumn herring are always more plentiful in the western than in the eastern part of the Baltic.

3. Spawning grounds in the southern Baltic

The spawning grounds of the autumn-spawning herring are situated in various places in the Gdansk Bay, and in the vicinity of Rozewie.

It has also been observed that the herring spawn in the neighbourhood of Rowy, Darlowo, and Niechorze, off the northern and eastern coasts of Rügen, and in the area to the south of Møen. However, it appears that the main spawning grounds of the autumn herring are located in the southern Baltic, somewhat farther to the north, near Bornholm and

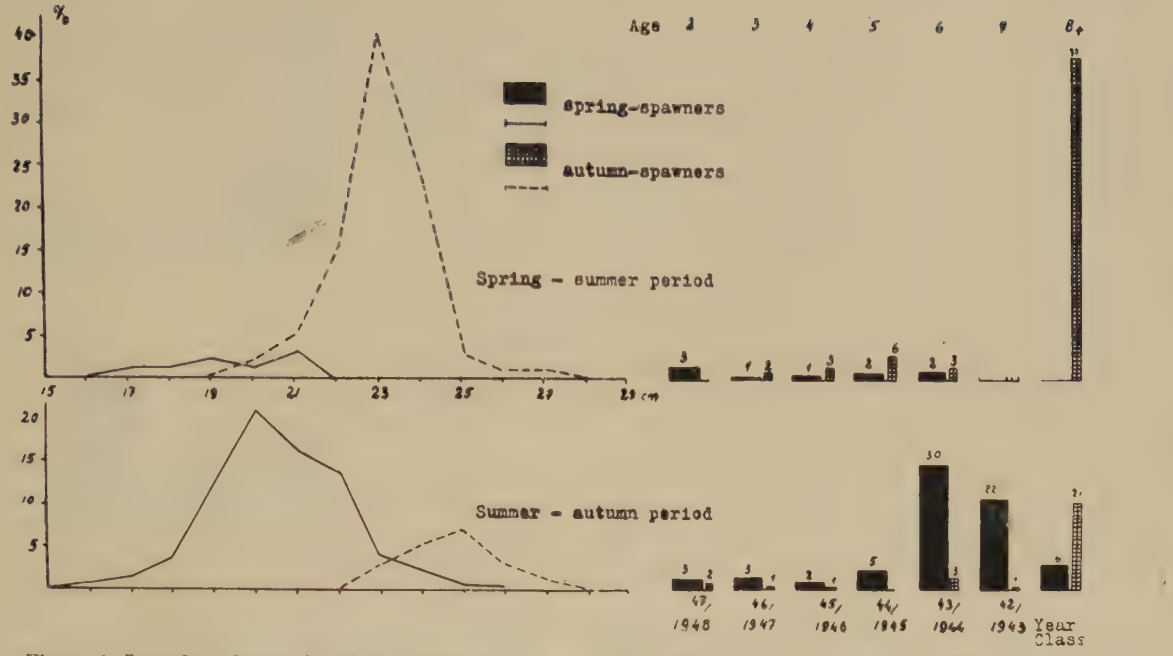


Figure 1. Length and age of spring and autumn spawners in Slupsk Furrow in different seasons of 1950.

in Hanö Bay. It is probable that autumn-spawning grounds may be found also on the Slupsk and Middle Banks.

Spawning herring are also encountered in set-nets in spring in the neighbourhood of Sopot and Orlowo, as well as in various places in the Puck Bay.

The second centre for spring spawning is located off the coast of Rügen, in the Pomorska Bay as far as Niechorze and in Szczecin Bay. It is only in the neighbourhood of Rowy and Ustka that small numbers of spawning herring are caught in spring.

As appears from the above, the main spawning of the spring herring takes place within the area of two bays, viz., Gdansk and Pomorska Bay, which are the outlets of the two largest rivers of this region, the Vistula and the Odra.

4. Fishery seasons

Formerly the herring fishery in the southern Baltic was primarily based on the exploitation of the above-mentioned coastal fishing grounds during the spawning periods.

As is well known, the herring after reproduction migrate from the coast towards the open sea, and it has been found that the densest concentration of feeding herring is met with in the waters farthest off shore. The feeding grounds are located in the southern part of Bornholm Basin, in Slupsk Furrow, in Gdansk Bay, and in the region to the west of Klajpeda.

The trawl fishery for herring is carried out during the whole year with various intensity. The yield of this fishery, as well as the character of the herring caught, changes nevertheless continually within the year. These changes take place with marked regularity. Owing to the age and race composition of the herring stock we may (as has been shown by J. Elwertowski (5) and J. Popiel (10)) distinguish between three distinct periods or seasons during the year:—

(a) The winter/spring period: from December—January to March—April. It is characterized by the predominance of young herring. A considerable proportion of the 2-year-old spring herring is already maturing to their first spawning. The yield of the fishery in that period is small. The fishing activities are concentrated in the southern part of Gdansk Bay and on those fishing grounds of the Bornholm Basin which are nearer to the Polish coast.

(b) The spring/summer period: from March—April to May—June. This period is characterized by the predominance of autumn-spawning herring which concentrate for feeding purposes in Bornholm Basin, Slupsk Furrow, and the region of Klajpeda. The old and large herring predominate among the autumn herring, but there is a small admixture of 1- and 2-year-olds. The admixture of spring herring is composed of both young, immature herring and adult fish, either maturing or spent. The yield of the trawl fishery on the above-mentioned fishing grounds is much higher than in the earlier period.

(c) The summer/autumn period: from June—July to November—December. This period is characterized by the predominance of spring herring of comparatively older age-groups (6-, 7-, and 8-year-olds).

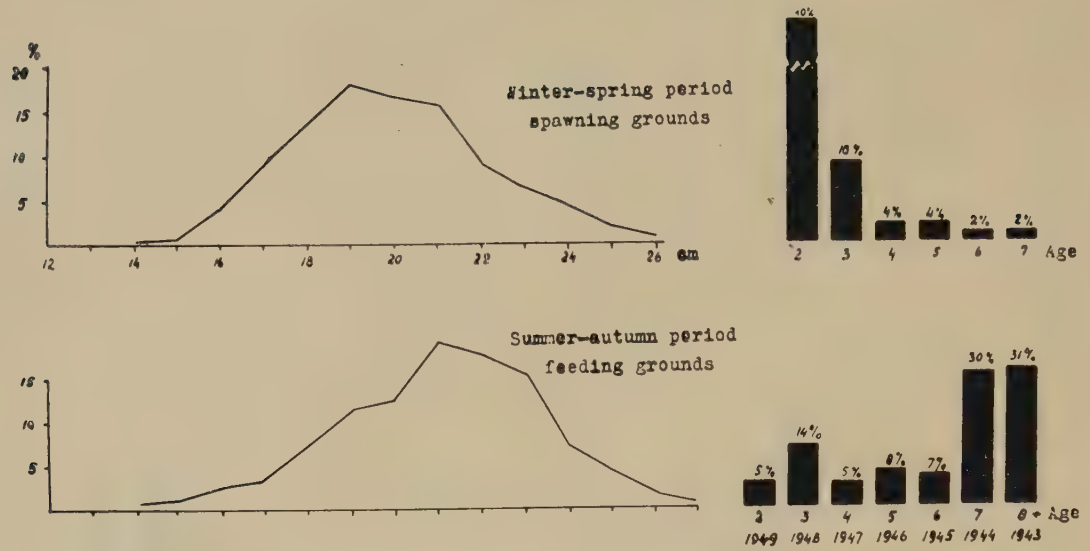


Figure 2. Length and age of spring spawners in Gdansk Bay in different seasons of 1950.

Besides these, a small number of autumn herring in the maturing stage or in the final phase of spawning still occur. The most numerous concentration is then found on the fishing grounds farther off shore, in Bornholm Basin, Slupsk Furrow, and the region of Klajpeda.

During periods (a) and (b) younger herring, besides the above-mentioned older fish, may be encountered on the fishing grounds near the coast. These fish originate from spawning which took place in the previous year. During September, a rather considerable number of small fish (0 group) also occur.

It appears from the above observations that conditions exist on the feeding grounds of the mature herring, located in the open sea, which are quite contrary to those observed on the spawning grounds. In the spring/summer period, that is, in the spawning period of the spring herring, the autumn herring predominate there, while in the autumn the spring herring are in the majority.

These relations are illustrated in Figure 1 by the example of the Slupsk Furrow. Corresponding differences were encountered in the race composition of the Bornholm Basin and Klajpeda fishing grounds. These differences were also observed in the successive years.

As a main result we have distinguished several herring concentrations, as follows:—

(i) spawning concentrations appearing in spring and autumn near the coast (coastal catches),

(ii) the winter/spring concentrations of young herring in the coastal region, but somewhat farther from the land (trawl catches), and

(iii) feeding concentrations of large, old herring occurring on the open-sea fishing grounds (trawl catches; spring/summer and summer/autumn).

5. Comparison of herring from different fishing grounds and seasons

A comparison of the characteristic features of herring occurring in the concentrations described above gives very interesting results.

The composition of the autumn herring stock observed on the spawning grounds is similar to that on the open-sea grounds. The same age-groups predominate in both localities. The young, immature herring predominate only in the winter/spring fishery. The growth-rate of the autumn herring is alike in all the concentrations, although the length curves of the particular age-groups from the deeper fishing grounds show many peaks. This would indicate a mixture of fish from the various parts of the Baltic.

Quite the reverse relations are found in the composition of the spring herring stock which appear in the concentrations described.

It has already been stated that the 1- and 2-year-olds predominate among the spring herring caught in the coastal regions of Gdansk Bay and Bornholm Basin during the winter/spring period. The 2-year-olds are already maturing for the first spawning. The age composition of the spawning stock changes somewhat towards the end of the winter/spring period. In the Pomorska Bay, for instance, the 3-year-olds predominate, and there is a considerable admixture of 2- and 4-year-olds. As regards Gdansk Bay the 2-year-olds predominate on the fishing grounds in the vicinity of Wisloujscie, just as in the trawl catches. On the other hand, in the Firth of Vistula and Orlowo the 3-year-olds predominate with a considerable admixture of 2- and 4-year-olds.

A common feature of the composition of spring spawners both in Gdansk and Pomorska Bays is the small numbers of herring more than 6 years old. The

Table 1
Ratio head/body length of the 4-year-old and older herring caught in Gdansk Bay

Ratio head/body length	Winter/Spring catches	Summer/Autumn catches
	Number of fish	
4·8—4·9	—	3
5·0—5·1	—	26
5·2—5·3	—	53
5·4—5·5	9	72
5·6—5·7	55	41
5·8—5·9	64	22
6·0—6·1	59	5
6·2—6·3	36	4
6·4—6·5	6	1
Total...	229	227
Mean...	5·916	5·456

growth-rate of the spring herring taken by trawl in the winter/spring period and of the herring from the spawning grounds is quite similar.

Quite a different stock composition is observed in the trawl catches in the summer/autumn period (Figure 2), when 6, 7, and 8-year-old herring clearly predominate on the offshore grounds. These age-groups were not encountered on the spawning grounds within the limits of Pomorska and Gdansk Bays. The Polish herring fisheries depend largely on this stock of fish. Figure 3 shows the age composition of this stock in the post-war period[1]).

The growth-rate of herring caught in summer and autumn differs considerably from that observed in spring on the Gdansk and Pomorska spawning grounds.

As appears from Figure 4, these differences are perceptible only in herring belonging to the older age-groups. The growth-rate of the younger herring is very similar in both periods. It is thus apparent that these young fish originate from the spawning grounds of Pomorska and Gdansk Bays. It is also evident from Figure 5 that the growth-rate of the older herring from the summer catches is distinctly slower in the first years of life only. The growth-rate attained in the third year is very similar for both types of herring. In the fourth year it is not the herring caught on the spawning grounds in spring that grows faster, but the fish caught in summer. The conclusion is that the growth-rate of the latter, being slower at first, is more uniform in the following years, however.

The differences in the growth-rate of the spring herring as described above, are clearly reflected in the structure of the scales.

When analysing the trawl-caught herring in the summer/autumn period, we were struck by the fact that the head seemed to be larger (in comparison to

[1]) The determination of the age of older groups was made on the basis of the narrow ring on the scales and otoliths in 1947. The 2-year-olds were excluded from the age composition because the occurrence of this group is not as a rule dependent on the abundance, but rather on the time and place of the catch. The proportion of this group fluctuates between 2 and 20 %.

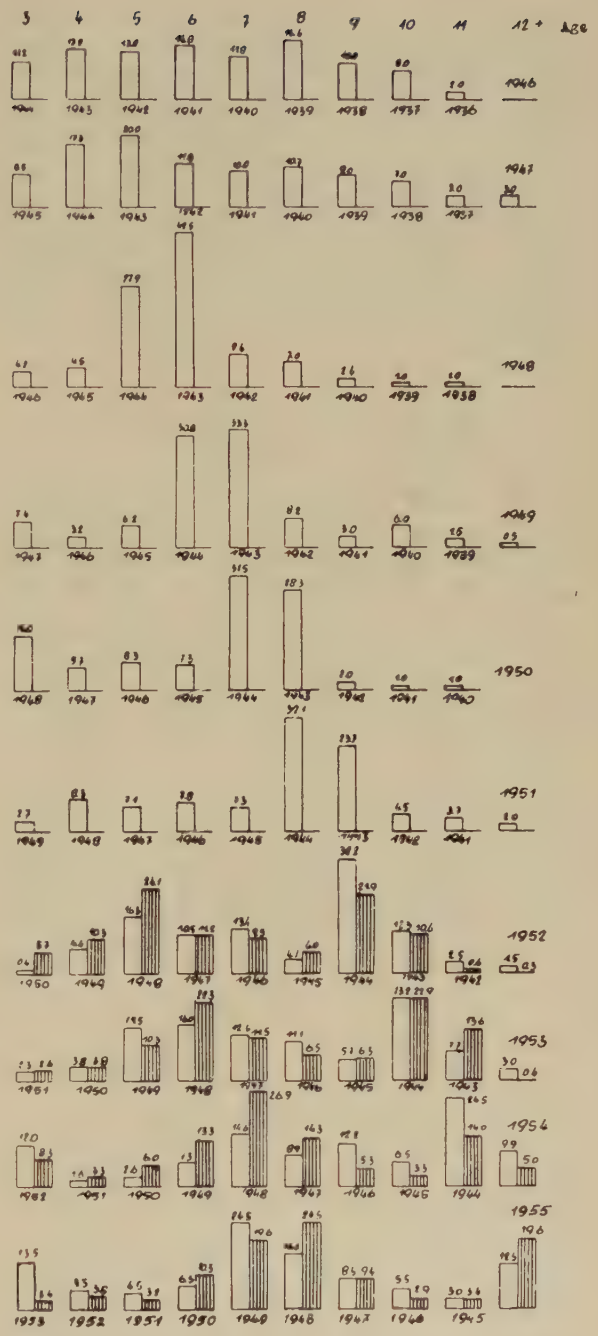


Figure 3. Age composition (%) of spring spawners taken in the summer/autumn catches on the open-sea grounds.
White columns = Gdansk Bay.
Striped columns = Bornholm Basin.

body length) than the head of the fish which appeared on the spawning grounds in spring.

The relative length of the head is no reliable feature by which to distinguish the particular groups of

herring since, as stated by HEINCKE (6), the head size decreases with increasing body length. Owing to this a comparison of measurements was limited to older fish of equal length.

The results of the measurements are compiled in Table 1. It appears from this table that the herring from the summer/autumn catches have a considerably larger head than those spawning off our coasts in spring. The mean length of the former goes into the length of the body 5·456 times while it is 5·916 times of the latter. A statistical analysis of the differences between the mean values can be expressed by the following equation, which plainly shows the actual difference:—

$$\frac{M_1 - M_2}{\sqrt{m_1^2 + m_2^2}} = \frac{0{\cdot}46}{\sqrt{0{\cdot}0186^2 + 0{\cdot}0158^2}} = 18{\cdot}9$$

The above considerations show that on the deep-sea fishing grounds of the southern Baltic and Gdansk Bay there appear, in the summer/autumn period, numerous accumulations of old, slow-growing herring. They are distinctive by their comparatively large heads. Judging from the state of the development of the gonads spawning took place in late spring. We did not observe such herring on the spring-spawning grounds in Gdansk or Pomorska Bays. They differ from the latter by a lower growth-rate, especially in their first years of life, and by a longer life.

The age and length compositions of these stocks is similar throughout the southern Baltic (Fig. 6). It must be supposed that these fish come to the southern Baltic waters from the north. Both the low growth-rate and the high age, which characterize these fish, support this supposition. It is known that the spring

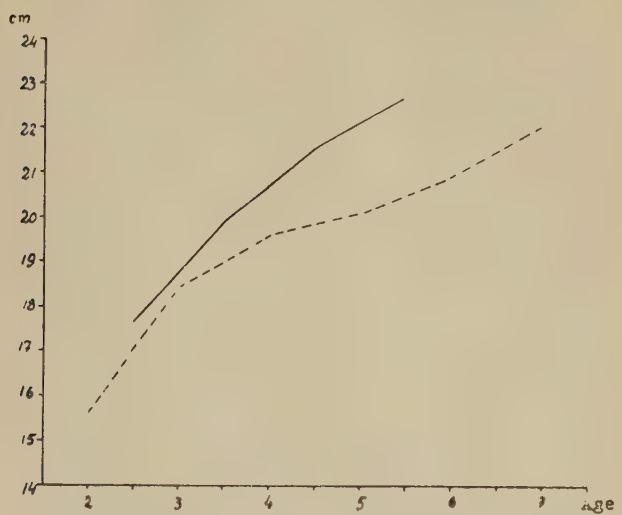


Figure 4. Average length of different age-groups of spring spawners from Gdansk Bay in the period 1946 to 1951.
——— on the spring-spawning grounds.
- - - - - - in the summer catches.

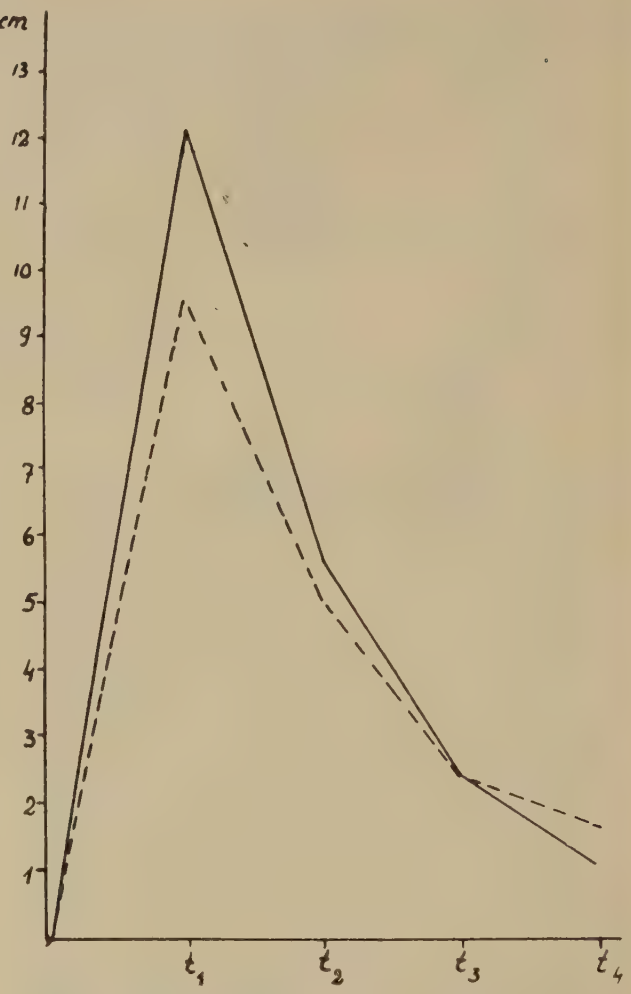


Figure 5. Annual length increment of spring spawners in Gdansk Bay.
——— on the spring-spawning grounds.
- - - - - - in the summer catches.

herring spawn intensively in May and June in the central Baltic near the Swedish coast in the vicinity of Gothland and Öland, as well as in Hanö Bay. It is possible that these herring after having spawned, migrate southward in search of food.

During this migration some shoals come right down to Gdansk Bay. Such great distance may probably be covered only by the strong, old fish. The young, slow-growing herring probably remain in the north and this explains why they do not occur in our waters. This opinion is confirmed by the fact that the herring described above appear on the fishing grounds farther to the north earlier than in Gdansk Bay. The presence in the southern Baltic, and even in Gdansk Bay, of enormous herring, more than 30 cm. long, described by HESSLE (7) as "giant herring", affords

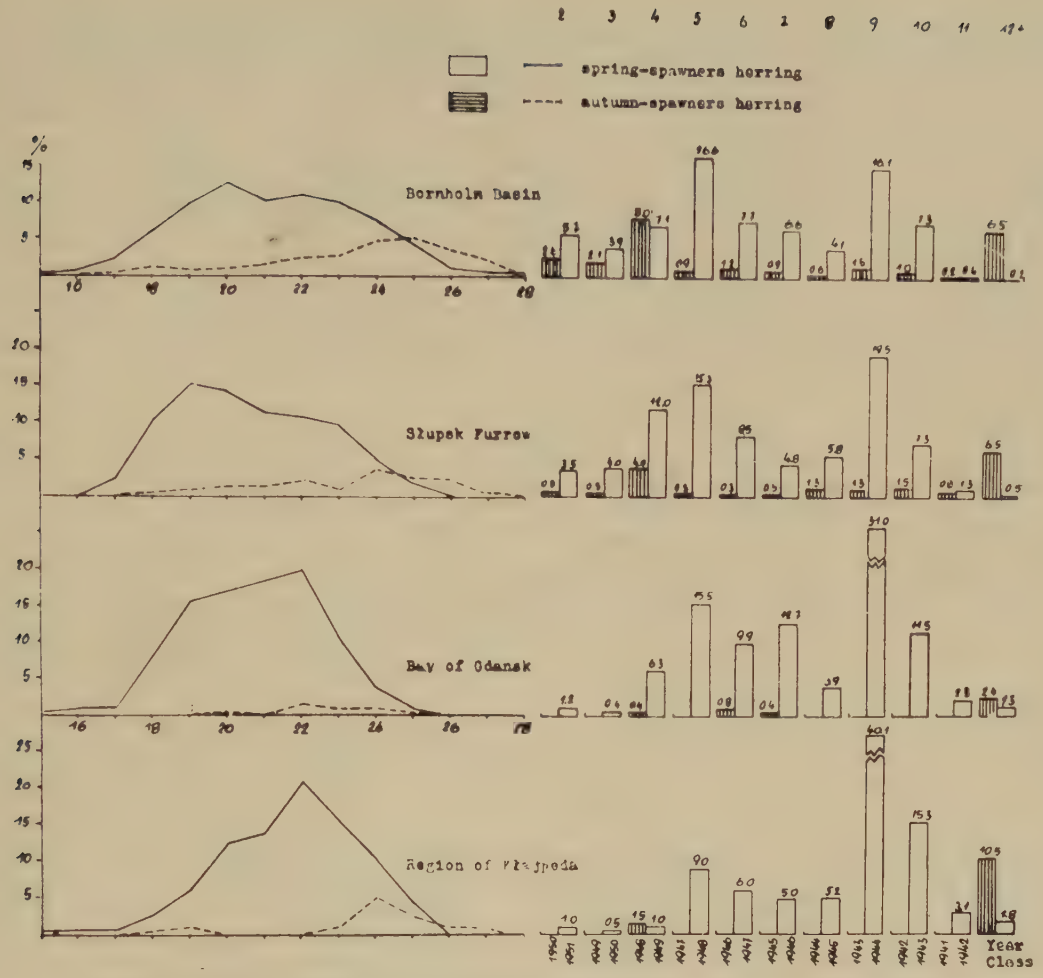


Figure 6. Age and length of spring and autumn spawners from the open-sea grounds in summer/autumn of 1952.

evidence of the fact that Baltic herring shift in a north-south direction. The "giant herring" appear in Gdansk Bay mainly in June—July. We hardly ever encounter autumn-spawning herring among these large fish. Their characteristic features are the same as given by HESSLE for the type of herring which occur in the fjords of middle Sweden. The largest fish we saw was 38 cm. long and weighed 480 g.; it was about 15 years old.

The mean number of vertebrae in the herring from different periods and regions of the southern Baltic is presented in Tables 2 and 3. It appears from Table 2 that:—

1. the number of vertebrae in the autumn-spawning herring increases towards the west. In Gdansk Bay the autumn herring have a slightly higher number of vertebrae than the spring herring;
2. the spring-spawning herring in Gdansk Bay have a distinctly lower number of vertebrae than those of Pomorska Bay. The VS is, however, almost identical with that observed in the Firth of Vistula herring;
3. the spring-spawning herring in Pomorska Bay have a higher number of vertebrae than the herring occurring in summer and autumn in Bornholm Basin and Slupsk Furrow, and
4. no great differences are found in the number of vertebrae in the Gdansk Bay spring herring in the various periods of fishing.

The last conclusion is not, however, confirmed by Table 3. As is known the number of vertebrae fluctuates considerably in the various broods. Consequently a comparison has been made in this table between the same two abundant broods caught in 1943 and 1944.

Table 2

Number of vertebrae in herring from various regions and periods of fishing in the southern Baltic

	Year of catch	Mean VS	Number of fish	Standard deviation	Standard deviation of the mean
Autumn-spawning herring					
Gdansk Bay	1945—1948	55·41	747	0·7290	0·0267
Słupsk Furrow	1949—1950	55·43	182	0·6902	0·0512
Bornholm Basin	1947	55·55	99	0·6555	0·0659
Spring-spawning herring Winter/spring					
Gdansk Bay	1945—1949	55·23	1,676	0·7303	0·0178
Firth of Vistula	1948—1949	55·20	168	0·7681	0·0593
Pomorska Bay	1950—1952	55·55	199	0·6843	0·0485
Spring-spawning herring Summer/autumn					
Gdansk Bay	1945—1949	55·22	1,732	0·7772	0·0187
Słupsk Furrow	1949—1950	55·39	147	0·7243	0·0597
Bornholm Basin	1949	55·36	187	0·6899	0·0504

Table 3

Number of vertebrae in spring-spawning herring of the 1943-44 year-classes in Gdansk Bay

Period	Age of fish	Mean VS	Number of fish	Standard deviation	Standard deviation of the mean
Winter/spring	2—5 +	55·23	827	0·7457	0·0259
Summer/autumn	2—4	55·17	192	0·7949	0·0574
Summer/autumn	5 +	55·31	412	0·7318	0·0361

It appears from the table that the old herring from the summer/autumn catches had a slightly higher vertebral count than the young fish. As is known from the considerations above these young herring are identical with those which occur on the spawning grounds in the winter/spring period. The above has been confirmed in Table 3.

Summary and Conclusions

In the southern Baltic we distinguish between three groups of herring, viz.:—

(i) The autumn-spawning herring. This fish spawns from the end of August to November. The mean number of vertebrae fluctuates about 55·5— with a decreasing trend towards the east. The growth-rate is liable to a similar trend, although some broods show similar lengths even in regions as separate as Bornholm Basin and Gdansk Bay.

In general, the stocks of autumn spawners in the southern Baltic do not differ essentially from one another. They are probably closely related to the autumn herring in the Belts and the Sound, whereas these fish have many features in common with the autumn herring of the North Sea. It may be supposed that there is quite a complete chain of autumn spawning herring stocks extending from the North Sea through the Belts and Sound right to the southern Baltic. These stocks gradually change their characters the farther east they occur.

(ii) The spring-spawning herring in brackish, inshore waters. The stock of herring spawning in Gdansk and Pomorska Bays belong to this group. The latter has already been described by Heincke (6) as the spring-spawning herring of Rügen. The characteristic features of these stocks are the fast rate of growth and the short cycle of life. Spawning takes place from March to May. The old fish are the first to arrive on the spawning grounds, and therefore the average length of the fish caught diminishes as spawning progresses.

In spite of considerable similarities the herring from the two bays constitute, no doubt, two separate stocks. They differ in vertebral counts. In Gdansk Bay, VS is about 55·2 while in Pomorska Bay it is 55·6. Besides, the Pomorska herring have a faster growth-rate and spawn somewhat earlier than the Gdansk herring. Both stocks are biologically similar to the fish which spawn in spring in the various bays of the western Baltic. Moreover, G. Krefft (9) links this fish with the spring herring which occur in the Sound and Belts and in the southern North Sea. Their spawning grounds are located in the estuaries of German rivers and off the coasts of Jutland. Herring with similar characters formerly occurred in the Zuider Zee.

(iii) The spring-spawning herring from the deep-sea fishing grounds. This fish differs from the above-mentioned by a slow growth-rate in the early years, a long cycle of life, and a comparatively bigger head.

The number of vertebrae of these herring varies greatly, but it would seem that they have a slightly higher count than those spawning in Gdansk Bay. The VS is, however, distinctly lower than in the Pomorska Bay herring.

There is a marked inclination towards migration. This herring group is probably closely related to the spring herring originating from the fjords and the open sea, e.g., the fjord herring and sea herring described by Hessle (7). They spawn mainly in May and June in the fjords and in the vicinity of the Isles of Gothland and Öland. These waters differ from the bays and river mouths of the southern and western Baltic in hydrographic conditions, structure of the bottom, and the character of the sea-bed. There may be a certain connexion between these herring and some local stocks living in the Norwegian fjords. The Lusterfjord stock described by O. Aasen (1) may prove this. It resembles closely the Baltic herring stock described above, in size, growth-rate, and length of life. The great difference in the number of vertebrae is undoubtedly caused by the higher salinity of the Norwegian fjords as compared to the Baltic Sea.

References

1. Aasen, O., 1952. "The Lusterfjord herring and its environment". Fiskeridirekt. Skr., **10** (2).
2. Cieglewicz, W., & Posadzcki, K., 1947. "Comparative studies of the spring and autumn spawning herring of the Gulf of Danzig". Ann. Biol., **2**.
3. Demel, K., 1928. "Wroznienie ras sledzi polawianych u naszych wybrzezy". Arch. Hydr. i Rybact., **3**.
4. Einarsson, H., 1951. "Racial analyses of Icelandic herring by means of the otoliths". Rapp. et Proc.-Verb., **128** (1).
5. Elwertowski, J., 1952. "Materialy do poznania podstaw biologicznych rybolowstwa sledziowego na Pomorzu Zachodnim". Prace M.I.R., 7.
6. Heincke, F., 1898. "Naturgeschichte des Herings". Abhandl. Seefisch.-Vereins, **2**.
7. Hessle, Chr., 1925. "The herrings along the Baltic coast of Sweden". Publ. de Circ., 89.
8. Kändler, R., 1942. "Über die Erneuerung der Heringsbestände und das Wachstum der Frühjahrs- und Herbstheringe in der westlichen Ostsee". Monatschr. f. Fischerei, 2.
9. Krefft, G., Schubert, K., & Sahrhage, D., 1955. "Der augenblickliche Stand der Erforschung des Nordseeherings mit besonderem Hinblick auf die Frage seiner Überfischung". Arch. Fischereiwiss., **6** (3/4).
10. Popiel, J., 1955. "Z biologii sledzi baltyckich". Prace M.I.R., 8.
11. Rannak, L. A., 1953. "Nerestowyje areały, nerest i ocenka moshchnosti pokoleni sałaki w wodach Estonskoj S.S.R." Trudy VNIRO, **26**.
12. Schneider, G., 1908. "Die Clupeiden der Ostsee". Rapp. et Proc.-Verb., **9**.
13. Spaskij, N. N., & Rittih, L. A., 1955. "Nekotoryje rezultaty rabot po izuchteniu biologii i razpredelenja sałaki w jużnoj Baltikie". Trudy Bałtijsk. Filiała VNIRO, 1.
14. Suworow, E. K., 1913. "K ichtiofaunie Bałtijskogo moria". Trudy Bałt. Exped., 2.

16.

Some Results of German Investigations on Herring Larvae

By A. Bückmann *and* G. Hempel

Summary*)

In continuation of earlier investigations (Bückmann, 1950) on the distribution of herring fry in the German Bight special observations in the Jade Estuary were carried out in the period 1948—1953. Catches were made with the Petersen young-fish trawl once or twice per month at 5—7 stations in the area. Herring larvae of different lengths entered the Jade in several waves from February to May.

I. Groups of larvae

On account of their modal length 4 larvae groups may be distinguished. In comparison with the observations in the open sea in pre- and post-war years it is possible to determine the presumable origin of these larvae groups:—

1. Larvae from the summer spawning in the western part of the central North Sea were met with in the Jade in February and March having a mean length of about 40 mm.

2. Smaller larvae, 30—35 mm. long, which presumably had hatched in autumn on the Dogger Bank entered the inshore area in March.

3. Two groups of different size ("ältere" and "jüngere Downslarven") may originate from the spawning places in the southern Flemish Bight. The larger specimens may be spawned in November—December. Their mean length is about 30—35 mm. at the time of entry into the Jade in April or May. The offspring of the January spawning in the eastern Channel appeared in the Jade only in single years, at the end of April or in May. They were then about 25 mm. long.

II. The number of vertebrae

Vertebral counts have been made on about 5000 larvae.

1. The distribution of the number of vertebrae does not fit the Error Curve as do the samples of adult herring. The variation curve is skew and peaked. Only in few cases we found a similar distribution in samples of 1-year-old herring.

2. As in pre-war years a correlation was stated between the mean number of vertebrae and the mean length of the larvae. In the 1952 year-class there was also some correlation between vertebral number and growth-rate: in a particular larvae group, presumably of uniform origin, the largest and probably fastest growing specimens exhibited a higher average count than the smaller ones.

3. These results give rise to a hypothesis: during the larval development some of the larvae with a low Vert. S. is eliminated from the group. Conceivably these are the variants of low growth. This results in an increase of the average number of vertebrae of the group. At the same time the degree of deviation from normal distribution of vertebrae decreases.

4. In consequence of these variations and changes of Vert. S. within a given larval group it is somewhat difficult to separate larval groups by their vertebral counts. The distinct difference found between the average number of vertebrae of pre- and post-war samples may be caused by differences in the length composition.

5. The determination of Vert. S. of whitebait in the Jade showed a slightly higher Vert. S. for the older herring than for the larvae of the same year-class. It is only in some years that a certain correlation between length and Vert. S. is apparent in 1-year-old herring also. It may be worth mentioning that the mean length of the whitebait was higher after 1950 than in the corresponding month of the previous years.

6. The number of vertebrae is inversely correlated to the water temperature during the first months of larval life (November, December).

7. Rearing experiments showed a similar negative correlation between the rearing temperature and the number of myotomes of yolk-sac larvae. Probably

*) The paper will appear in full in Helgoländer Wiss. Meeresunters., **6** (1).

there is also a temperature dependence of the myotome count after hatching.

8. Our observations led to the assumption that Vert. S. and, probably other meristic characters, are subject to modifications which are assumed to occur only within limits fixed by heredity. The mean number of vertebrae in a sample of a given larval group may be due to interactions of inheritance and modifications caused directly or indirectly by environmental factors. Moreover selection processes and distribution of the larvae in space and time are supposed to influence the average values. After metamorphosis the selection combined with mixing processes and, on the other hand, the separation in different groups may continue. Thus the Vert. S. of spawning shoals are assumed to be caused by a complicated system of influences. Only some of these influences are known as yet.

17.

Meristic Characters in the Young Herring of the Bløden Ground Area

By K. Popp Madsen

Summary*)

Countings of keeled scales and vertebrae have been carried out on the 1949 and all subsequent year-classes. Average values of single samples lie within the following limits, $K_2 = 14{\cdot}30$—$15{\cdot}15$ and VS = $56{\cdot}34$—$56{\cdot}80$. The total average of all counts are, $K_2 = 14{\cdot}793$ (9,275) and VS = $56{\cdot}572$ (9,988). There is a general increase in mean number of K_2 with increasing age, and—at corresponding age and season of the year—there is a decrease in K_2 from year-class 1949 to year-class 1954.

The mean number of VS shows no general trend.

*) The full paper will be published in Medd. Danmarks Fisk.- og Havunders., N.S., **2**.

18.

Stock Composition of the Young Herring in the Bløden Ground Area

By K. Popp Madsen

Summary*)

The fishery is divided into two seasons: a spring fishery in January—May and an autumn fishery in July—October. The spring fishery is based upon fishes with one and two winter-rings on the scales, while fishes with one winter-ring are by far the most important component during the autumn. The age composition in spring has shown a steady decline in the percentage of $2^1/_2$-year-old herring from 1951 to 1955. In 1956 the percentage increased again. The autumn fishery does not show any marked differences from one year to another.

The length distributions show the same pattern of variation between year-classes both in L_1 measurements, at $1^1/_2$ and at $2^1/_2$ years of age. There is further an indication of a negative correlation between the average length of the Bløden herring and the number per landing of 3-year-old recruits in the East Anglian fishery for corresponding year-classes.

This seems to indicate that the changes observed in the Bløden stock reflect changes taking place before the herring arrive on the Bløden Ground. Most probably they are due to variations for different year-classes in the relative strength between early and late autumn spawned components in the Bløden stock, i. e., between Bank herring and Downs herring.

*) The full paper will be published in Medd. Danmarks Fisk.- og Havunders., N.S., 2.

19.

The North Shields Fishery 1949–1955

By A.C. Burd

Summary

The Shields fishery is, in the main, a recruit fishery based on herrings in their third summer. At the commencement of the season the scales of these recruits bear two winter-rings and gradually the summer growth is laid down. New recruits, which can be distinguished by the state of their gonads and the amount of growth on the scale, continue to enter the fishery for almost the whole of the season.

It was shown that the three-year-old recruits represent a mixture of fish with high and low l_1s. The fish with the high l_1s will spawn earlier in the year than those having low values of l_1 as can be seen by comparison of their maturity stages. These two groups correspond with the Bank and Downs herring distinguished by Cushing and the Early and Late Autumn Spawners described by Bertelsen and Popp Madsen from the nursery grounds east of the Dogger.

The spring fishery on the Bløden consists of fish of age-groups I and II, i.e., having one or two winter-rings respectively. The II-groups do not appear in any great quantity in the autumn fishery. It is possible that these are the source of the supply of recruits to the north-east coast fisheries.

An estimate of the onset of first maturity was made by taking the percentages of Hjort Maturity Stage I in each cm. group of two- and three-year-old fish. The mean lengths of fish at the 50% point were shown to be similar irrespective of age.

The continuous supply of fish from the edges of the Dogger into the north-western North Sea is probably maintained by the differential rate at which fish on the Bløden approach the critical length. As they do so, they then move away from the nursery areas. Bertelsen and Popp Madsen have shown that when there are many Early Autumn Spawners in an age-group the mean length is higher than when there are few. There is then a possibility for a partial separation of the two components—Early Autumn Spawners (Bank herring) and Late Autumn Spawners (Downs herring). In fact the recruit two-year-olds which occur in the Shields fishery are always Bank herring having high l_1s.

20.

Selection of Representative Samples in a Herring Fishery

By I. D. Richardson

Summary

The paper is concerned with pointing out the variability between samples taken throughout the Whitby herring season. The variability in age between samples is shown to be reflected in changes in average length for age, vertebral count, and l_1 size.

It has been suggested that there may be a pattern within each season and that variations probably result from separate groups of fish entering the fishing area as the season progresses. The parallelism between the proportion of each age-group within a sample and the change in the length coincident with this change in age, suggests that there are separate groups of fish moving into the fishery. This movement is confirmed from echo-surveys in the area, which show a general movement of the main echo density from north to south within the fishing area, occurring at least twice and usually more often during the season.

The change in the composition of the samples is further reflected in the change in maturity. Using Hjort's maturity scale, there is a progression from stage V to stage VI—VII during the season followed, after one sample of predominantly stage VII fish, by a return to stage V and later, stage VI. These changes in maturity composition are coincident with changes in age and length composition discussed earlier.

These are samples taken from a gear which is non-selective at least so far as mesh is concerned and the differences between samples exist within a short time period.

Some of the variation between samples but not all, is probably due to the numbers sampled, but before ascribing to a particular fishery a diagnostic character such as vertebral number, etc., the variation between samples taken throughout the season must be recognized, or a completely false value may be given. No attempt has been made in the paper to assess the sizes or distribution of the samples throughout the season, which it would be necessary to take in order to obtain an accurate figure for the catch of the fishery during the season.

21.

Some Changes in Vertebral Counts of Herrings

By D. H. Cushing
Fisheries Laboratory, Lowestoft

The validity of the distinction between the Bank and Downs herring stocks (or the Bank and Channel stocks of Schnakenbeck, 1931) has often been discussed in terms of mean vertebral counts (Buchanan-Wollaston, 1933). The vertebral count of the Bank herring lies between 56·40 and 56·50 and that of the Downs herring ranges from 56·50 upwards (Johansen, 1924; Lissner, 1934); recently, Ancellin (1951) has noticed that fish spawning at Sandettié had vertebral counts of 56·41 in 1951 and so it might be concluded that the Bank herring extended to the Straits of Dover. It will be shown that this event was probably not related to any change in stock migration and that vertebral counts may be used to confirm the separation of the two stocks, already set up on other evidence (Cushing and Burd, in press).

Material and methods

Since the war, samples of vertebral counts of each year-class have been taken at Lowestoft; Table 1 shows them arranged by age and by year-class. No estimate of error is made, because of the low number of frequency classes available and the skewness of the distributions (Buchanan-Wollaston, 1933).

Certain vertebral counts from the North Sea spawning grounds are available in the *Annales Biologiques* (reproduced from Table 1 in Cushing, 1955). Figure 1 shows some of these observations; each, with the exception of those taken off East Anglia, was taken on a spawning ground and each mean is derived from samples of more than 100 fish.

Results

I. The stability of vertebral counts in the East Anglian fishery

In Table 1, the vertebral counts of fish of one age in different years are compared with those of fish of one year-class for a number of years. It is immediately obvious that the range is much less within a year-class than that within a series of samples of one age in different years. Again, the differences between successive year-classes are sometimes great and are consistently maintained, e. g., those between the 1946, 1947, 1948, and 1949 year-classes. Another point is that there may be a slight trend upwards from 1941 to 1955.

The argument of this paper is based on a general application of Tåning's results with the trout (Vedel Tåning, 1950), namely, that vertebral counts are determined environmentally at some time near spawning; one would then expect to find differences between year-classes, particularly amongst the recruits to the adult fisheries. It is, however, surprising that the differences persist, the year-classes apparently retaining their identity throughout their lives. Thus, the vertebral count of a year-class is a sensitive index of two characters:—

(1) an environmental factor on the spawning ground, probably temperature;
(2) the integrity of a year-class, i.e., the extent to which it does not mix with other elements during the course of its life. Thus the 1950 year-class is perhaps less mixed than the 1948 class, merely because the range is less.

It might be claimed that within a year-class, the vertebral count gradually changed as more mixture took place. Table 1 shows the counts arranged in an order of increasing age within each year-class.

(The figures in heavy type show two samples from 1947; in this year there may have been a genuine admixture of some more northern fish.)

From Table 1 it appears that there is no trend in vertebral count with age. Consequently it is possible that once the year-class is made up as it leaves the nursery ground, it retains its identity throughout life. In other words, there is no immigration into the year-

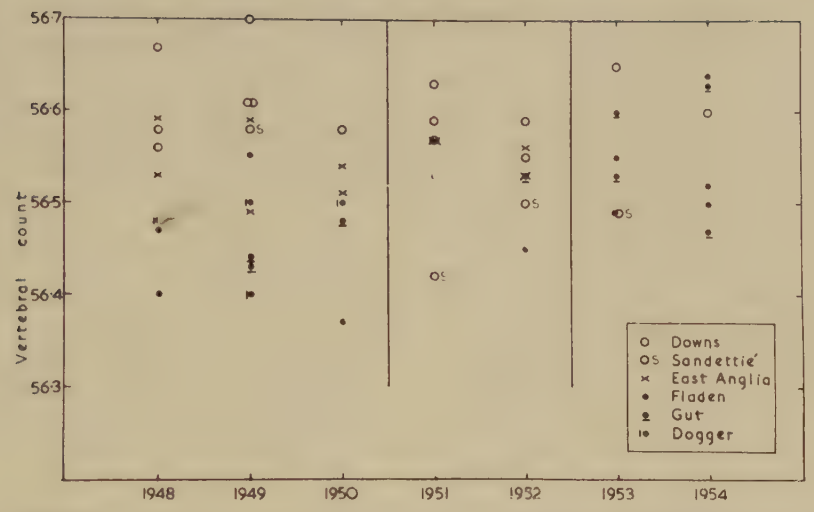


Figure 1. Vertebral counts from various North Sea spawn-ing or pre-spawning grounds. The three periods are 1948—50, before the change in recruitment; 1951—52, the period of change; and 1953—54, after the change in recruitment.

Table 1
The vertebral counts of each age-group in the East Anglian fishery, arranged by year-classes

Age	3	4	5	6	7	8	9
Year-class							
1940	—	—	—	—	56·48	56·46	—
1941	—	—	—	56·41	56·51	56·50	56·43
1942	—	—	56·45	56·54	56·56	56·48	—
1943	—	**56·39**	56·45	56·49	56·53	—	—
1944	**56·33**	56·57	56·52	56·48	—	—	—
1945	56·57	56·66	56·63	—	56·64	56·63	—
1946	56·48	56·44	56·44	56·51	56·42	56·47	—
1947	56·55	56·65	56·58	56·60	56·52	56·68	—
1948	—	56·51	56·47	56·56	56·58	—	—
1949	56·54	56·54	56·58	56·55			
1950	56·54	56·60	56·59	—			
1951	56·53	56·57	—				
1952	56·57	—					

class after it has been recruited into the fishery. If there were emigration, one would expect to find the trends reproduced in the fishery which received the emigrants.

II. The recent changes in vertebral counts

Figure 1 shows the average vertebral counts of all year-groups by different years from the major spawning or pre-spawning grounds in the North Sea. Three groups of fish are distinguished:— (1) the Downs group, comprising samples from Sandettié and the eastern Channel, (2) the Bank group, comprising the Fladen, Gut, and Dogger, and (3) the East Anglian fishery, which by vertebral count is apparently intermediate between the Bank and Downs groups.

Because a change in recruitment took place in 1951—52, I have distinguished three periods, 1948—50, 1951—52, and 1953—54.

(a) The first period, 1948—50. It is assumed that a high vertebral count is associated with a low native temperature, and *vice versa*.

The vertebral counts are arranged on the ordinate of Figure 1 in decreasing order of magnitude, which corresponds to the following order in sampling:— Eastern Channel, Sandettié and the Dogger, Fladen, Gut group. From the *Hydrographic Synoptic Charts* published by the Council, the following temperatures have been extracted for August—October on the Dogger, for November on the Sandettié, for January off Boulogne, and for February off Dieppe:—

Year	Dogger Aug.-Oct. °C.	Sandettié November °C.	Off Boulogne January °C.	Off Dieppe February °C.
1950.....	11—16	12	—	—
1951.....	12—15	13	7	6
1952.....	10—15	11	8	6
1953.....	12—16	13	6—8	6
1954.....	11—14	13	8	5
1955.....	—	—	8	—

From the differences in temperature alone we would expect to find the order in vertebral counts given above. As the East Anglian fish spawn at Sandettié and off Boulogne (Hodgson, 1929, 1950), we would expect that the East Anglian vertebral counts would be intermediate between those from the Dogger and those from Boulogne. Hence there is no need from this evidence to postulate admixture of adult fish from the Dogger into the East Anglian shoals. Similarly, the separations made by Le Gall (1935) into Groupe "Dyck Sandettié", and Groupe "Manche Orientale", I and II, may be explained on this basis alone; of the array of characters presented by Le Gall

(including a set of very similar age distributions) the only differences were in vertebral count.

(b) The second period, 1951—52. In 1951, the lowest vertebral count of all was found in samples from the Sandettié bank. In 1952 the differences between the two groups, Bank and Downs, were not very great.

From Table 1 and Figure 1 it will be observed that the 1946 year-class had a low vertebral count in any case. These fish were five years old in 1951; Ancellin (1951) has shown that there was a vertebral count of 56·42 on Sandettié which is the same as that of the five-year-olds in East Anglia (56·43).

(c) The third period, 1953—54. The most remarkable point here is that the vertebral counts of the Bank herring have increased from perhaps 1952 and certainly from 1953. But the vertebral counts of the Downs herring have not changed. In timing, it is likely that this increase in vertebral count is related to the change in recruitment which took place in 1950—51. Not only did the pattern of recruitment to the Downs stock change at this time but that to the Bank stock changed also, resulting in a marked increase in the abundance of recruits to the Buchan pre-spawning fishery. (Parrish and Craig, ICES Special Meeting on the East Anglian herring, 1956).

Popp Madsen (ICES Herring-Race Meeting, 1956) has shown that the magnitude of recruitment to East Anglia is associated with the modal length reached by the II-group fish in the Bløden autumn fishery, i.e., that a high recruitment is related to a low modal length and that, conversely, a low recruitment is related to a high modal length.

The following hypothesis is suggested. Larvae reach the coastal waters bordering the eastern nursery ground in a continuous stream from the Dogger and the Straits of Dover, over a period of about six months. Similarly, there is a stream of recruits leaving the nursery ground between spring and late summer, the early ones of which move north towards the Buchan pre-spawning fishery. The later recruits in the late summer and early autumn move into the East Anglian fishery. The separation between the two groups is possibly an effect of the length reached at a particular time.

Thus the very early recruits were almost certainly spawned in summertime and the very late ones were spawned in winter. Between the extremes some winter-spawned fish move north to join the Bank stock, as a result of improved growth and of the increased quantity of early spawning in November at the Hinder Bank (which is an effect of the increased representation of recruits at three years old in the Downs stock). Hence, not only does the magnitude of recruitment to the Bank stock increase, but also the vertebral counts tend to rise.

It is well realized that the increase might be attributed to a northward migration of older fish from the Downs stock, with effect from 1952 or 1953. The Buchan pre-spawning fishery, which contains Bank recruits, in May, June, and July 1954 showed the following vertebral counts:—

	May	June	July
Fraserburgh	56·58	56·63	56·50
Peterhead	56·61	56·68	56·59

The majority of these fish were three-year-olds and most were in the early part of the fishery, in maturity stage I (Parrish *et al.*, 1956). Thus the recruits to the northern fisheries since 1952 also have high vertebral counts, which have not been derived by admixture of older fish from the south.

Discussion

The relation between the Downs and Bank stocks should now be reconsidered. It will be recalled that the two stocks were separated on three points (Cushing, in Cushing & Burd, in press). These are:—

1. the differences in age-distributions,
2. the differences in the distribution of tags, and
3. the differences in vertebral counts.

We may now add that the adult year-classes of Downs herring retain their identity throughout their lives, with no immigration; for the reasons given above we believe that emigration is unlikely. This concept of adult integrity accounts for the three points of difference given above.

The points of similarity between the Downs and the Bank stocks find their source in a more or less common recruitment of three-year-olds. The recent increase in abundance of northern three-year-olds, and the recent increase in the vertebral counts of Bank fish, are parts of the same change in recruitment already described for the East Anglian fishery.

Thus there are two great groups of herring, sharing their sources of recruitment from immature fish, remaining separate during their adult lives, and spawning separately. Yet their spawning products may not all join the parent stock, but some may go to the other group. Hence recruitment, growth, and mortality might well have different values in the two groups, as indeed is shown by the differences in age distributions. It is concluded that the Bank and Downs stocks are separate units of management.

References

Ancellin, J., 1951. "La pêche française en Sud de la Mer du Nord et de la Manche orientale". Cons. Internat. Explor. Mer, Ann. Biol., **7**: 141.

Buchanan-Wollaston, H. J., 1933. "Some modern statistical methods: their application to the solution of herring race problems". J. Cons. Int. Explor. Mer, **8**: 7.

Cushing, D. H. 1955. "On the autumn-spawned herring races in the North Sea". J. Cons. Internat. Explor. Mer, **21** (1): 44.

— 1957 (in press). "The Downs Herring", in: Cushing, D. H. & Burd, A. C. "On the herring of the southern North Sea". Fish. Invest., Ser. 2, **20** (11).

Hodgson, W. C., 1929. "Investigations into the age, length and maturity of the herring of the southern North Sea. III". Fish. Invest., Ser. 2, **11** (7).

— 1950. "The East Anglian herring fishery in 1949". Cons. Internat. Explor. Mer, Ann. Biol., **6**: 175.

Johansen, A. C., 1924. "On the summer- and autumn-spawning herrings of the North Sea". Medd. Komm. Danmarks Fisk.- og Havunders., Ser. Fiskeri, **7** (5).

Le Gall, J., 1935. "Le hareng *Clupea harengus* Linné. 1. Les populations de l'Atlantique nord-est". Ann. Inst. Océanogr., N.S., **15**: 1.

Lissner, H., 1934. "On races of herrings". Cons. Internat. Explor. Mer, **9** (3): 346.

Parrish, B. B., Baxter, I. G., McPherson, G., & Buchan, J. D., 1956. "Scottish Fisheries, 1954". Cons. Perm. Internat. Explor. Mer, Ann. Biol., **11**: 127.

Parrish, B. B., & Craig, R. E., 1956. "Recent changes in the North Sea herring fishery". ICES, Spec. Meet. on the East Anglian Herring Fishery, Pap., 24.

Popp Madsen, K., 1956. "Stock-composition of the young herring in the Bløden Ground area". ICES, Herring Ctee, Pap., 45.

Schnakenbeck, W., 1931. "Zum Rassenproblem bei den Fischen". Zeitschr. f. Morphol. u. Ökol. der Tiere, **21** (3/4): 409.

Vedel Tåning, Å., 1950. "Influence of the environment on number of vertebrae in teleostean fishes". Nature, **165**: 28.

22.

On the Distinction between Herring Races in the Autumn- and Winter-Spawning Herring of the North Sea and English Channel by means of the Otoliths and an Application of this Method in Tracing the Offspring of the Races along the Continental Coast of the North Sea

By K. H. Postuma *and* J. J. Zijlstra

Introduction

Several authors (Jenkins, Lissner, Einarsson) have stated that the nucleus of the sagitta, the largest of the three otoliths, is different in summer and spring spawners. According to Jenkins and Einarsson, otoliths of spring spawners show opaque centres in transmitted light. On the other hand, in summer, autumn, and winter spawners, hyaline centres are observed under the same circumstances. Lissner came to similar conclusions, but in some cases he observed small hyaline nuclei in the otoliths of spring spawners. Einarsson, in a quantitative study, found that the vast majority of spring spawners possessed otoliths with opaque centres.

In a herring otolith hyaline and opaque zones alternate; every year a hyaline and an opaque zone seem to be added to the otolith. In this way the age of the fish can be determined.

According to Lissner the hyaline zones are built up in the period from August till May, coinciding with slow growth of the fish. The opaque parts of an otolith, in his opinion, were formed in a period of intensive metabolism from May till July. The fish is growing fast in this period.

As the larvae of spring spawners are hatched just before the period of abundant food and have a fast growth-rate, the centre of the otolith would be opaque.

The larvae of summer, autumn, and winter spawners, however, would hatch in the period of a relative scarcity of food and would have a slow growth-rate, resulting in a hyaline appearance of the otolith centre in transmitted light.

If the explanation of the difference in appearance of otolith nuclei of spring and autumn spawners is correct one might expect that differences in size of the otolith centre might exist within the group of summer, autumn, and winter spawners. In this group the time of hatching varies considerably, the larvae hatched earliest being about 5—6 months older than those hatched at a late date. The onset of the period of intensive growth, with the consequent formation of an opaque zone in the otolith, probably occurs at about the same time in both late and early hatched larvae. We would expect the length of the periods of slow growth and the formation of a hyaline part in the otolith to be very different, ranging from about 4 to 9 months. Provided that the growth-rates are similar, different sizes could be expected in the hyaline otolith centres.

Zijlstra (p. 134) gives evidence of the existence of different stocks in the group of autumn and winter spawners. Each stock is supposed to have its own spawning area and spawning period. In his opinion these are maintained by a tendency of the herring to return for spawning to the ground where they were born. The majority of the spawning shoals, visiting an area, have originated from former spawnings in that area.

As to the problem of the otolith centres two points in the above hypothesis are of importance: firstly, it is thought that at least the majority of the members of a "race" spawning during a given period originate from a spawning in that period; and, secondly, the "races" have different spawning periods. These two points should give rise to differences between the "races" in the mean sizes of the hyaline otolith centres. The members of a "race", spawning early in the season, should have, on the average, larger hyaline centres than those spawning later in the period of slow growth. One of the aims of this investigation was to study this point. The expected differences between the stocks with different spawning periods being observed, support would be given to Zijlstra's hypothesis.

If it proved to be possible to distinguish between the stocks by the otolith, then this method could be applied in tracing the offspring of the different stocks on the nursery grounds. In this paper a first attempt in this direction has been made.

Material and Methods

The material collected consisted of adult herring and immature herring. The adult herring were caught on three spawning grounds in the southern North Sea and English Channel, viz., S.W. Dogger area, the Sandettié area, and the English Channel. These are probably the main spawning grounds in the area. Only herring in maturity stages, V, VI, and VII were used in this investigation, the idea being, that these herring spawn in the area where they are caught. The material was collected in 1954 and 1955. The total numbers of fish amounted to 1000 individuals, equally divided among the spawning grounds.

The immature herring belonged mainly to the 0-group, the age of the individuals varying mainly between 1 and $1^1/_2$ year. The samples were collected during the winter of 1955—1956, and were caught in the following regions:—

1. The inlets of **Zeeland,** in the southern part of Holland.
2. The Dutch coast at **IJmuiden,** up to 40 miles off the coast.
3. The coastal area and the inlets in the north of Holland (Waddensea region).
4. The vicinity of Wilhelmshaven, off the German coast.
5. The **Horns Reef** area, near Esbjerg (Danish coast).
6. The Swedish Skagerak coast, in the vicinity of **Lysekil.**

From the last three areas samples were obtained by courtesy of the German, Danish, and Swedish fishery laboratories. Their most helpful assistance is much appreciated.

The hyaline otolith centres were measured with a binocular microscope, magnification × 32. In the microscope an eye piece micrometer was fitted. Each scale unit of the micrometer represented 0·0327 mm., with the magnification used. The measurements were made to the nearest scale unit. In order to increase the visibility of the structures in the otoliths, a liquid was used permeating the otolith rapidly. In order to observe if this type of liquid changed the otolith structures in the course of time, for instance by an apparent enlarging of the hyaline centre, otoliths were kept for varying periods in xylol. No change in structure was observed. Later xylol was replaced by anisole (methoxybenzene).

From the otolith centres the radius was determined. Near the centre of the nucleus a little bubblelike structure was observed in most otoliths. The distance from this "bubble" to the distal edge of the hyaline zone was measured. This edge is characterized in the following way: from the centre of the otolith nucleus a radiating structure can be observed in the hyaline area. At the edge of this area the structure diffuses in all directions and a dense network is formed. This boundary was used as the outer limit for the measurements.

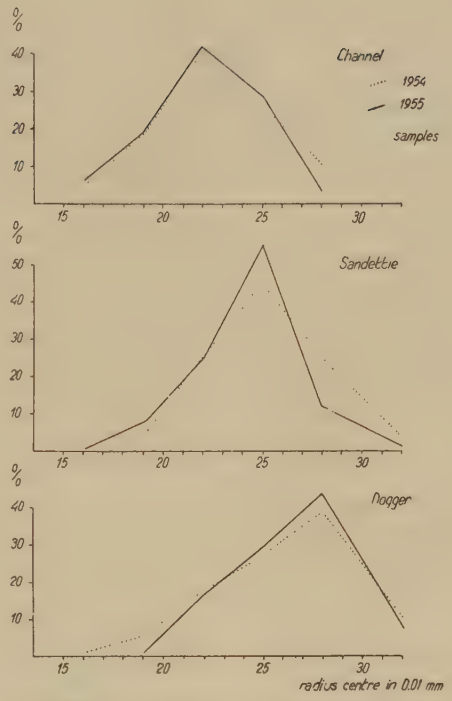


Figure 1. Radius of otolith centre.

Data and Results

1. Spawning herring

For each of the three spawning grounds Dogger, Sandettié, and the Channel the distributions of the radii measurements of the otolith centres were calculated for each year of sampling separately. In Figure 1 the results are shown. It may be noticed that differences exist between the individual spawning grounds. In both 1954 and 1955 the Dogger has, on an average, the largest otolith centres (average size of radius: *1954: 0·273 mm., 1955: 0·276 mm.*), the Channel has the smallest otolith centre (*1954: 0·235 mm., 1955: 0·230 mm.*), and the Sandettié shows an intermediate one (*1954: 0·261 mm., 1955: 0·253 mm.*). The X^2-test was used to see if the differences observed fell within the sampling variation. The test revealed that the differences between the three spawning areas could not possibly be caused by sampling variation and were almost certainly due to other causes (for all cases tested: $p < 0{\cdot}001$).

The data of 1954 and 1955 are compared for each spawning area in Figure 1. In general they show a remarkable similarity, although some differences exist. Again the need was felt to test with the X^2-test, if these differences could be attributed to sampling variation. This proved to be the case for Dogger and the Channel, for Sandettié, however, a p as low as $\pm$ 0·01 was found.

Due to the small samples, pooled data for individual year-classes were used in calculating the distributions

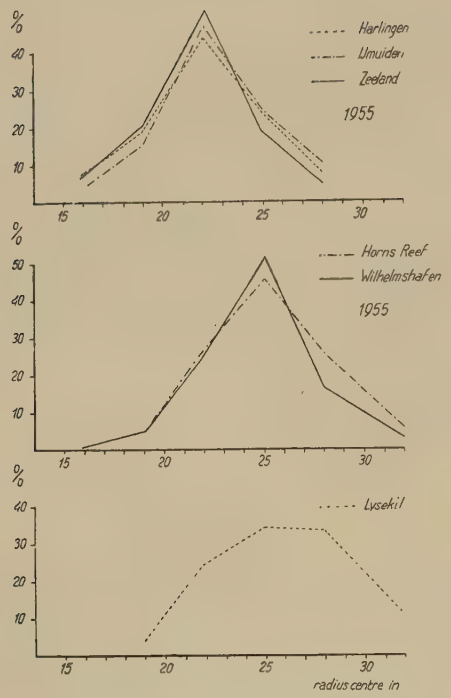


Figure 2. Radius of otolith centre in whitebait.

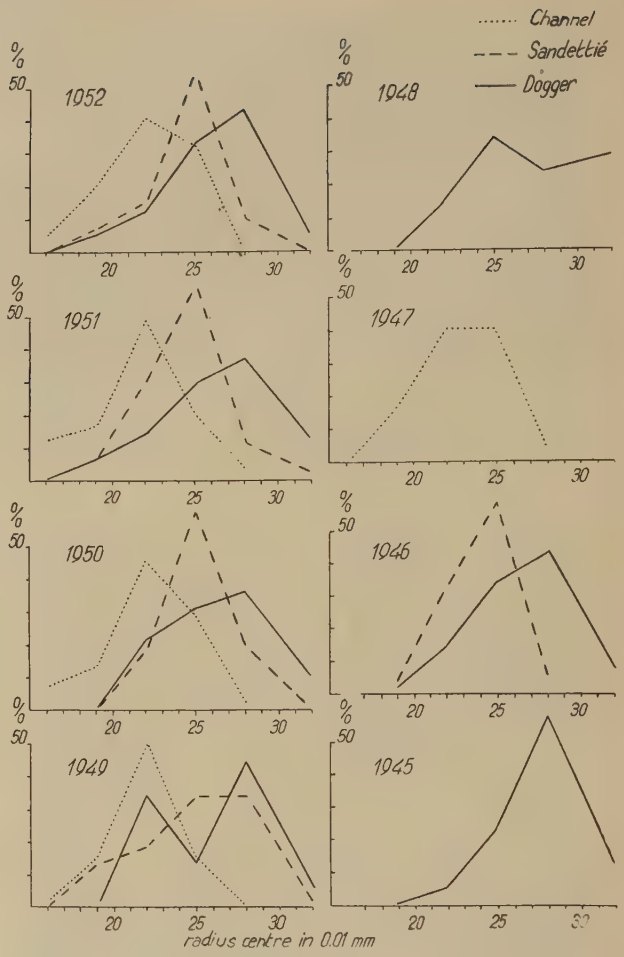


Figure 3. Radius of otolith centre of various year-classes.

of the radii measurements of otolith nuclei for each spawning area. The results are given in Figure 3. Even after pooling the data of 1954 and 1955, most distributions are based on a small number of observations. Some variations may be noticed between the distributions of the year-classes on one spawning ground. Again the X^2-test was used to enable us to see if these differences were statistically significant. For both Dogger and Channel the differences observed fell within the possible sampling variation, but for Sandettié a significant difference was found ($p = 0{\cdot}03$).

From the data and their statistical reliability, we may conclude that differences in the size of the otolith centres do exist between the spawners of the three areas. These differences are the more striking as the variation in the data from a spawning ground, both between the two years of sampling and between the year-classes, was found to be small.

As for the cause of the differences in the size of the otolith nuclei, mentioned in the introduction, they may be connected with the differences in the time of hatching. Fish hatched early in the period of slow growth (August—May) might be expected to exhibit a larger hyaline otolith centre than fish hatched late in this period. In the following table times of spawning in the areas observed are compared with the average size of the otolith centres of their spawners.

The time of spawning and the size of otolith centres are related in the way mentioned above. This result

Area	Time of spawning	Mean radius of otolith centre mm.
Dogger	September—October	0·275
Sandettié	November	0·257
Channel	December—January	0·231

supports the hypothesis that time of hatching is responsible for the differences in the size of the otolith nuclei. However, as we are dealing here with spawning herring, it also means that the majority of the herring spawn in the same season as that in which they were hatched. And as spawning season and spawning grounds seem to be strongly connected, it might mean that the herring returns for spawning to its native ground. As such it supports ZIJLSTRA's hypothesis.

The observation that only small variation is found between the year-classes on one ground might be due to the fact, that the spawning periods in the areas are the same each year. However, this implies that the growth-rate each year during the period between the hatching of the larvae and the formation of the opaque zone in the otoliths is the same.

2. Whitebait samples

Whitebait (0-group herring) were collected in the area from Zeeland (in the south of Holland) to the Swedish Skagerak coast, in order to explore the possibilities of using the otolith method to trace the offspring of the spawning groups. Most samples came from the Dutch coast, mainly from three regions: Zeeland, IJmuiden, and Waddensea.

In Figure 2 the distribution of the radii measurements of the otolith nuclei are shown for the different areas. The following table gives the radii measurements of the hyaline centres per area:—

	Mean radius mm.	Number of observations
Zeeland (southern Dutch coast) ..	0·226	125
IJmuiden (central Dutch coast) ..	0·237	136
Wadden (northern Dutch coast) ..	0·231	135
Wilhelmshaven (German coast) ...	0·257	100
Horns Reef (Danish coast).....	0·263	95
Lysekil (Swedish Skagerak coast).	0·272	124

Compared with the data of the three spawning grounds (Channel r = 0·231 mm., Sandettié r = 0·257 mm., Dogger r = 0·275 mm.) and with Figure 1 (compare Figures 1 and 2) we may conclude that the whitebait along the Dutch coast in the year of sampling was very similar to the spawning herring of the Channel area, in both mean and distribution.

The samples from Wilhelmshaven and Horns Reef show a great similarity with the spawning herring of the Sandettié area in the size of the otolith centres. The data of the Lysekil sample, finally, might indicate a mixture of Sandettié and Dogger herring, for both the mean and the distribution are more or less intermediate between these two groups.

However, it is possible, that young herring from other spawning grounds live in the areas from where our samples originate. For a more careful study it is necessary to know the distribution of the sizes of otolith centres of the main spawning groups in the North Sea, combined with a more intensive sampling of immature herring.

Although no conclusive evidence could be drawn from our present material, we are hopeful that it will be possible to obtain in this way important information about the distribution of the offspring from the spawning grounds.

Summary

Several authors (Jenkins, Lissner, Einarsson) have mentioned the existence of differences in the otolith centres of spring and autumn spawning herring, the spring spawners having opaque otolith centres and the summer spawners hyaline centres. These differences are attributed to differences in the time of hatching, the opaque parts in a herring otolith seem to be formed between May and July, and the hyaline parts between August and May.

These facts led us to consider the possibility that differences in the size of the hyaline otolith centre occurred between herrings spawning at different times in the period during which the hyaline centre is formed. For these herring the time of hatching determines the length of this period, and consequently differences in the size of the otolith centre could be expected.

Herrings were studied in this respect, originating from three spawning areas, namely Dogger, Sandettié, and the Channel. It was realized, that differences of the kind described above, could only be found if the majority of the herring returned for spawning to the ground where they were born.

An analysis of the material revealed that Dogger herring had on an average the largest otolith centre, then came Sandettié, and finally Channel. These observations are in good agreement with the hypothesis; on the Dogger spawning takes place in September—October, on Sandettié in November, and in the Channel in December—January. Furthermore, the differences proved to be constant in successive years and for each year-class. This result gives support to the belief that the time of hatching is responsible for the differences in the size of the otolith centre and to the idea that the majority of the herring return for spawning to the grounds where they hatched.

Only a small variation was found to exist between the distributions of the character of the different year-classes on one ground. This may be due to rather fixed periods of spawning.

A first attempt to distinguish between the offspring of the individual spawning grounds using this method gave a promising result.

Bibliography

Einarsson, H., 1951. "Racial analysis of Icelandic herrings by means of otoliths". Rapp. et Proc.-Verb., **128** (1).

Erdmann, W., 1936. "Untersuchungen über die Zusammensetzung der Heringsschwärme in der nördlichen Nordsee". Rapp. et Proc.-Verb., **102**.

Immermann, F., 1908. "Beiträge zur Altersbestimmung der Fische II". Wiss. Meeresunters., N.F., **8**, Abt. Helgoland.

Jenkins, J. T., 1902. "Altersbestimmung durch Otolithen bei Clupeiden". Wiss. Meeresunters. N.F., **6**, Abt. Kiel.

Lissner, H., 1925. "Die Altersbestimmung beim Hering mit Hilfe der Otolithen". Ber. Deutsch. Wiss. Komm. Meeresforsch., N.F., **1** (2).

Zijlstra, J. J., 1957. "On the herring 'races' spawning in the southern North Sea and English Channel (preliminary report)". Rapp. et Proc.-Verb., **143**.

23.

On the Herring "Races" Spawning in the Southern North Sea and English Channel

(Preliminary Report)

By J. J. Zijlstra

Introduction

For a long time it has been realized that the herring living in North Atlantic waters may be divided into a number of "races". In this connexion a "race" is thought to be a more or less self-maintaining unity (Heincke, 1898). The "races" can be distinguished by differences in the meristic characters, due to either genotypic or phenotypic factors.

The question whether such "races" also occur in the group of herring spawning from July till January in the North Sea and English Channel, has been argued for many years. This is probably largely due to the special pattern of spawning grounds and spawning seasons found in this group. Spawning starts in July—August in the area along the Scottish N.E. coast and moves then gradually southwards in the course of the year to other grounds, ending in the English Channel in December—January. The spawning seasons on the different grounds overlap in several cases and some of the spawning areas are close together.

In the extensive literature on the subject contradictory views are found concerning the "racial" composition of this group. For instance, Hodgson considered the group to be more or less a unity, because he concluded from his data that an intensive interbreeding took place between the offspring from different spawning areas of the group. Other investigators, however, thought the group to be composed of at least two "races" (Schnackenbeck, Tesch, Le Gall, and Wood).

The two extreme possibilities for the "racial" status of the group are that either each ground is used by its own "race" for depositing the eggs, which means that herrings hatched on a certain ground return to the same ground for spawning, or that the interbreeding of herrings, hatched in different areas, is so strong, that the whole group has to be considered a unity.

Chart 1. Showing the sampling areas.

Between these two extreme alternatives one could imagine intermediate possibilities, for instance a partial interbreeding in relation to the geography of the area.

The "race" problem is of great importance for some aspects of herring research, for instance for population studies and the study of the migration routes of the herring (Cushing, 1955). Therefore, it seemed worthwhile to start new investigations on the "race" question of the North Sea herring spawning between July and January.

As the question of interbreeding seemed to us a vital point, it was decided to sample herring in

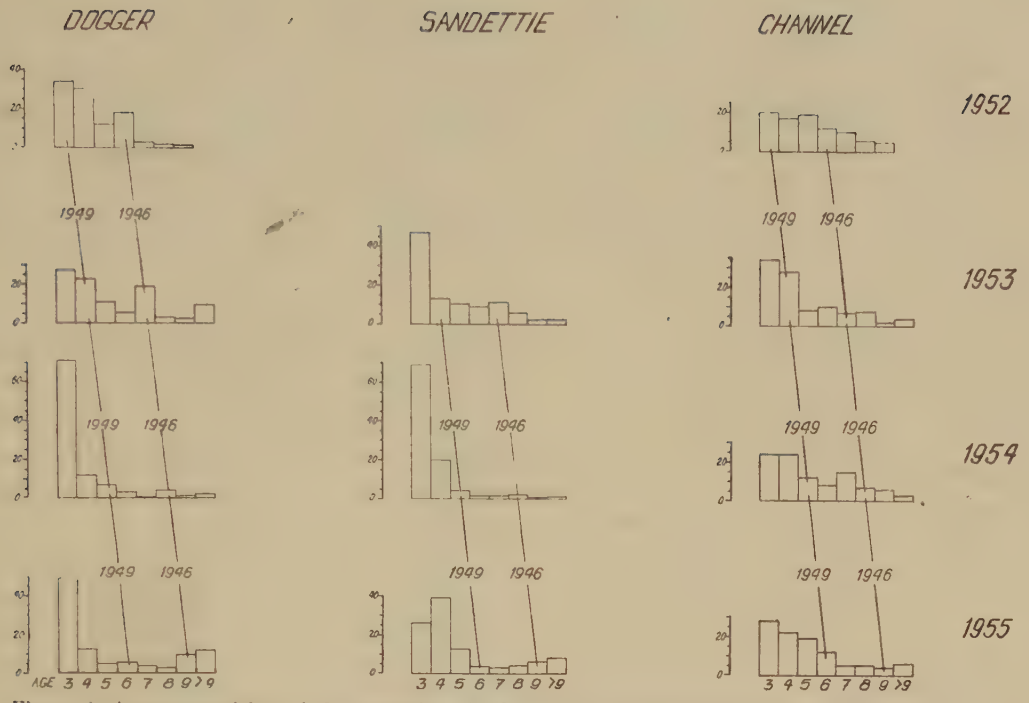


Figure 1. Age composition of the spawning shoals on the Dogger, Sandettié, and Channel grounds in 1952—1955.

spawning condition in the different spawning areas of the group.

We had to restrict the number of spawning grounds selected for sampling. Sampling was carried out in the S.W. Dogger area, on the Sandettié grounds, and in the English Channel (Chart 1). The areas mentioned are probably the principal spawning grounds in the southern North Sea and English Channel, as indicated by the distribution of catches of spawning herring (running roe and milt) by both Dutch luggers (drift-net) and trawlers (data not published). Data from German catches in 1953 gave the same impression (Sahrhage, 1954). Samples were collected partly from our research vessel and partly from catches of commercial trawlers. All herring were trawl caught.

Of the herring caught, only those in maturity stages V—VII were used for this investigation (Hjort scale). These herrings were considered to be spawners of the sampling area. This was of special importance for the Dogger area, where a mixing of all maturities was found, whereas on the other two grounds the samples consisted almost entirely of stage VI herring.

The material was collected from 1952 to 1955. The 1955 data have only been partly worked up. In the Sandettié area sampling started in 1953.

The material has been analysed with regard to four characters:— age distribution, vertebral counts, L_1 distribution, and growth. In the next section each of these characters will be considered with reference to three questions:—

1. Do differences exist between the three spawning grounds?
2. Are the data in successive years the same or different in one spawning area?
3. If differences occur, how can they be explained?

Results

Age distribution

The age distributions of the spawners of the three areas are shown in Figure 1, separately for the four years of sampling. Unfortunately, the method of sampling in 1952—1954 was not fully suited to give an exact representative picture of the age distribution of the herring stocks occupying the different grounds for spawning. Samples were taken when the opportunity arose, either at sea or in the market. This type of sampling might easily result in a rather inaccurate picture of the age distribution, especially as the number of samples is small, as was often the case in this investigation. This is probably due to the great variation in length and age distribution of the different herring shoals on a spawning ground. The age distributions of 1955 are probably much more accurate, as measures were taken to meet the difficulties in sampling. The age distributions in Figure 1 for this reason give no consistent picture, in some years the younger age-groups seem to dominate, and, in other years, the older age-groups.

However, in spite of these imperfections it is still

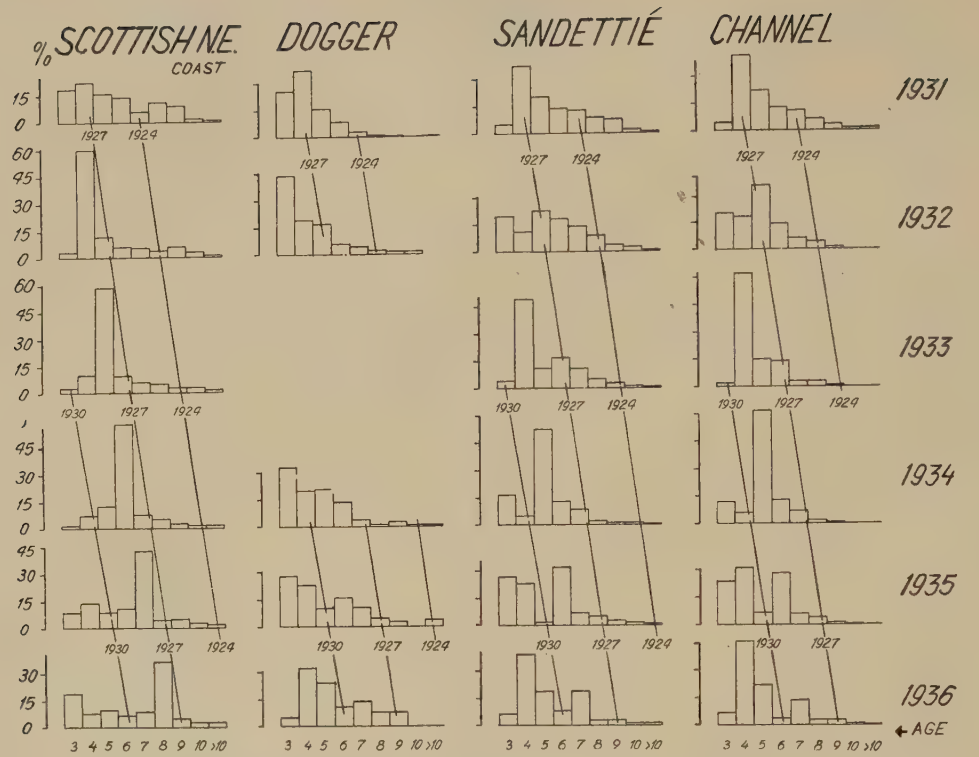


Figure 2. Age compositions of the spawning shoals of the Scottish N.E. coast, Dogger, Sandettié, and Channel in the period from 1931 to 1936.
(Data from Wood, Erdmann, and Le Gall.)

possible to distinguish consistent differences in year-class strength, when comparing the data of the three areas. This is especially clear for the year-classes of 1946, 1947, and 1948. On the Dogger ground the 1946 year-class is dominant in all four years of our investigation, and is much stronger than the 1947 and 1948 year-classes; the 1948 year-class is probably somewhat stronger than the 1947 one. In the Sandettié area the 1946 year-class is also a good year-class, but the difference from 1947 is less marked; the 1947 year-class is stronger here than the 1948 one. On the Channel spawning grounds 1947 may be noticed to be a dominant year-class, probably somewhat stronger than 1946 and certainly much stronger than 1948.

The picture is less clear for the other year-classes, due to the variations caused by inaccurate sampling. Comparing the Dogger and Channel areas it might be that the 1949 year-class on the Dogger is relatively good, while the 1950 year-class is fairly strong on the Channel grounds. In 1955, when sampling was done in a much more accurate way, the 1952 year-class (recruits) was found to be rather weak in the Channel area and especially on the Sandettié grounds, but on the Dogger it proved to be a fairly good year-class.

By comparing data from the literature similar differences could be traced in previous years for other areas. Data from Wood, Erdmann, and Le Gall, for the spawning grounds along the Scottish N.E. coast, the Dogger area, the Sandettié ground, and the Channel area, are shown in Figure 2. They concern the age distributions in the years 1931—1936. The most striking point in Figure 2 is the very different age distribution of the spawning shoals of the Scottish N.E. coast compared with those of the other grounds. On the Scottish spawning grounds the 1928 year-class dominated in the years 1932—1936, on the other grounds it was only a weak year-class. The differences between the other three grounds are less clear. In all three groups the 1927, 1929, and 1932 year-classes were relatively good, year-class 1929 being particularly strong in the Sandettié and Channel areas. The 1928 and 1930 year-classes were very weak on both Sandettié and Channel grounds, on the Dogger, however, the differences between the strong and weak year-classes were much less pronounced.

When comparing these data we have to keep in mind that it is not quite certain that we are dealing with pure spawning shoals. Wood mentions in his paper that his samples were taken from spawning shoals, Le Gall's samples consisted mainly of spawning and spent fish, while the Dogger samples, according to Erdmann, contained all possible maturities,

although the maturity stages V—VII were dominant.

Although more evidence might be found in the literature, I believe it sufficient to show that:—

(a) different age distributions may occur in the different spawning concentrations of the North Sea herring spawning from July till January;
(b) the relative strength of the individual year-classes is essentially the same on one spawning ground in successive years.

These two facts indicate, that mainly the same herring return every year for spawning in a certain area. In other words, the majority of the herring must return to the spawning area, where it has spawned in previous years. Our data do not suggest that a great deal of mixing takes place after the herring has come to spawn for the first time. In that case a gradual disappearance of the differences should have been observed.

As to the cause of the differences in the relative strength of the year-classes in the different spawning concentrations, there are possibly several explanations. One of them could be that the herring returns in general to the ground where it hatched. In that case the differences could be attributed to different survival rates of the broods of the three spawning areas. From this material, however, it is impossible to decide whether this is the right explanation.

Vertebral counts

The vertebral counts were the only meristic character used. They were calculated per year-class, for each spawning area and for each year of the investigation. In Table 1 the results are shown as means. It may be noticed, that differences seem to exist between the vertebral counts for the three spawning areas, for the individual year-classes in one spawning area and, finally, for the same year-class in different years.

All differences are relatively small, below 0·4 of a vertebra. In order to see whether they could be due to sampling variation, the *t*-test was applied.

In the first place the differences in vertebral counts between the spawning areas were tested. This was done for each year-class by pooling the data for the different years of sampling. Of 19 cases tested only three proved to differ significantly.

However, a comparison of the vertebral counts of the three areas shows that in general the Dogger has the lowest mean, the Channel the highest, while the Sandettié is intermediate or about the same as the Dogger. The data for the 1949 year-class are the only exception to this rule. It was therefore decided to pool the data of each spawning area and to test the distributions again. The means of the vertebral counts for the three areas were then:— Dogger: 56·53, Sandettié: 56·55, Channel: 56·62.

The *t*-test showed that the vertebral counts for Dogger and Sandettié did not differ significantly. The differences between Dogger-Channel and Sandettié-Channel, however, could not be attributed to chance variation ($p < 0{\cdot}001$ and $0{\cdot}001 < p < 0{\cdot}01$).

Table 1
Mean Vert. S. per year-class for three years of observation

(Between brackets the number of observations, on which the mean is based. Means, based on less than 25 observations have been omitted.)

Year of sampling	Year-class 1951	1950	1949	1948	1947	1946	1945
Dogger							
1952.....	—	—	56·64 (157)	56·56 (170)	56·62 (66)	56·54 (104)	—
1953.....	—	56·51 (234)	56·60 (240)	56·38 (122)	56·50 (58)	56·49 (210)	56·48 (33)
1954.....	56·52 (295)	56·51 (53)	56·68 (25)	—	—	—	—
Total...	56·52 (295)	56·51 (287)	56·62 (422)	56·48 (302)	56·56 (125)	56·50 (329)	56·43 (61)
Sandettié							
1953.....	—	56·52 (152)	56·63 (43)	56·66 (32)	56·48 (27)	56·46 (35)	—
1954.....	56·56 (487)	56·45 (143)	56·59 (32)	—	—	—	—
Total...	56·56 (487)	56·49 (295)	56·61 (75)	56·60 (43)	56·57 (37)	56·46 (48)	—
Channel							
1952.....	—	—	56·62 (135)	56·64 (109)	56·67 (129)	56·64 (84)	56·71 (68)
1953.....	—	56·65 (150)	56·53 (127)	56·68 (34)	56·66 (43)	56·64 (28)	56·67 (33)
1954.....	56·60 (169)	56·53 (154)	56·62 (83)	56·54 (59)	56·62 (107)	56·59 (49)	56·57 (40)
Total...	56·60 (169)	56·69 (304)	56·59 (345)	56·63 (202)	56·65 (279)	56·63 (161)	56·66 (141)

This result is supported by literature data. Several authors mention the vertebral counts of the Dogger herring to be lower than those of the Channel herring. Le Gall has often mentioned the vertebral counts of the Sandettié spawners to be very similar to those of the Dogger stock.

The variance in the vertebral counts of the individual year-classes on the same spawning ground proved to be statistically significant for both Dogger and Sandettié, in the Channel it might be due to sampling errors.

Finally, the variance in the vertebral counts for the same year-class, made in successive years on one spawning ground, was tested. Of 13 cases tested only one proved to have a p as low as 0·05 (Dogger: the 1948 year-class). In order to compare the variance in the vertebral counts in the different years on one spawning ground, the data of each observation year were pooled. No statistically significant differences could be shown in this case.

The last point, that the differences in the vertebral counts between the different observation years may be caused by sampling errors only, agrees with the

conclusion drawn from the age distributions, that at least the majority of the herring return for spawning to the area where they spawned for the first time.

The differences in vertebral counts between the different spawning concentrations could be accounted for as follows:—

If the herring in general return to the ground where they have hatched, then the differences in vertebral counts might be of either genotypic or phenotypic origin. The first explanation is suggested by Heincke and Schnackenbeck, the latter by Davis, Hodgson, and Runnström. A third possibility is that the differences are partly due to genetic factors and partly to differences in the habitat.

If the hypothesis of the purely genetic origin were true, the differences in vertebral counts would indicate the occurrence of stocks with different genes for the character on Dogger, Sandettié, and Channel. However, a difference was found in the vertebral counts for the individual year-classes in one spawning concentration. With a purely genetic cause for the differences, this must mean a mixing of the "races" on the spawning grounds. In that case the differences in genetic factors would disappear and this would be against the hypothesis. We mention here the possibility of some sort of isolating mechanism, but we do not think this to be very likely.

The other hypothesis was, that the number of vertebrae in a herring is affected in some way by the conditions of the habitat and that the differences found in vertebral counts are at least partly of phenotypic origin. Experiments with other fishes (*Salmo trutta*, *Lebistes*, *Fundulus heteroclitus*, *Pleuronectus platessa*) by Smidt, Vedel Tåning, Gabriel, and Dannevig make this assumption very likely. The experiments revealed a clear influence of some environmental factors, temperature being the most important one. The number of vertebrae proved to be determined in the egg stage, high temperatures giving a low value and low temperatures giving a high number of vertebrae. With herrings, these experiments were never performed, due undoubtedly to difficulties in rearing the herring larvae, but in view of the experimental results just mentioned an influence of temperature on the number of vertebrae in herring is very likely. This being accepted, the number of vertebrae would be determined by the temperature on the spawning ground at the time the eggs are developing. Differences in vertebral counts between the spawners of two spawning grounds might then be expected when the temperatures on the grounds are different at spawning time and when the majority of the spawners on a ground have hatched on this ground. A correlation between the vertebral counts and the temperature in the spawning areas in the spawning seasons must then be expected, which provides a method for testing the hypothesis.

A comparison between the vertebral counts and the mean temperatures in the spawning seasons for Dogger, Sandettié, and Channel for the period 1946—1951 confirms the hypothesis, that low vertebral counts go with a high temperature and *vice versa*, as is shown in Table 2 (mean temperature from *Bulletin Hydrographique*, published by ICES).

Table 2

Area	Vertebral counts	Mean temperature	Period
Dogger.....	56·53	13·4° C.	1946—1951
Sandettié...	56·55	12·0° C.	1949—1951
Channel....	56·62	10·6° C.	1946—1951

The above mentioned differences in the vertebral counts between the individual year-classes in one spawning area could possibly also be attributed to different temperatures in the years of hatching. Table 3 shows the vertebral counts of different year-classes with the corresponding temperatures (data from *Bulletin Hydrographique*).

Table 3

Year-class	Dogger		Sandettié		Channel	
	Vert.S.	°C.	Vert.S.	°C.	Vert.S.	°C.
1951.....	56·52	12·7	56·56	12·4	56·60	11·3
1950.....	56·51	12·7	56·49	12·0	56·59	9·6
1949.....	56·62	15·2	56·61	11·6	56·59	12·1
1948.....	56·48	13·5	—	—	56·63	11·4
1947.....	56·56	14·0	—	—	56·65	10·0
1946.....	56·50	12·2	—	—	56·63	9·7

From the table it is clear that no correlation exists between the vertebral counts and the temperature in the year of hatching. A calculation showed no significant correlation for either Dogger or Channel. However, when the data of all spawning grounds were taken together a highly significant correlation was found ($p = 0{\cdot}001$) with $r = -0{\cdot}77$. This last result is in good agreement with the assumption. That it is much better than that obtained for the individual grounds may be due to the wider temperature range and the more extensive data.

By comparing from the literature data it was possible to show again a relationship between the vertebral counts and the temperature on the spawning grounds in the spawning seasons. The vertebral counts for different spawning grounds were mainly collected in the period between 1930—1938 by Le Gall, Runnström, and Wood.

The temperature data were obtained from the "Provisional monthly mean charts", provided by the Service Hydrographique of ICES. Table 4 gives the results.

From this material a correlation coefficient was calculated; $r = -0{\cdot}906$, $p < 0{\cdot}001$.

All data given so far showing the relation between the vertebral counts and the temperature are combined in Figure 3. The correlation coefficient for the total material was found to be $r = -0{\cdot}85$ with $p < 0{\cdot}001$. In my opinion it is reasonable to conclude from this evidence that a negative correlation between the vertebral counts of a spawning concentration and the

Table 4

Spawning area	Vert. S.	° C.	Period	Author
S.W. Norway	57·35	5·0	Febr.—April	Runnström
Shetlands	57·05	7·0	Febr.—March	Runnström
Firth of Forth	56·99	6·0	Febr.—April	Wood
Channel (south)	56·71	8·5	Dec.—Jan.	Le Gall
Channel (north)	56·58	9·5	December	Le Gall
Sandettié	56·55	11·5	November	Le Gall
Dogger	56·44	12·9	Sept.—Oct.	Wood
Scottish N.E. coast	56·42	13·2	August	Wood
Berwick coast	56·40	13·0	August	Wood
Shetlands	56·43	12·5	August	Wood

temperature in the area in the spawning season probably exists.

This conclusion is corroborated by Bückmann, who found a negative correlation for the vertebral counts in herring larvae and the temperature in the neighbourhood of the spawning area in the year the larvae were collected. Bückmann, however, found the best relationship with temperatures occurring about 1—2 months after the end of the spawning season. Runnström reported a possible negative relationship between temperature and salinity with the vertebral counts for the spring spawners in the northern North Sea.

One objection can be made against the relation between the vertebral counts and the temperature on the spawning grounds. The temperatures used are estimated means of the surface temperature in a fixed period of the year in rather large areas. What is needed, however, are the temperatures at the bottom at the time and place of spawning. This might somewhat change the relation shown in Figure 3.

That a negative correlation was found between the vertebral counts and the corresponding temperatures on the spawning grounds supports the assumption that differences in vertebral counts between the different spawning concentrations may be at least partly due to different temperatures on the grounds. At the same time it confirms the idea of the majority of the herring returning for spawning to the area where they have been hatched.

If the herring selected its spawning ground regardless of the place where it hatched, I cannot think of a reasonable explanation for both the differences in the vertebral counts and the negative correlation, previously demonstrated.

L_1 distribution

The lengths of the herrings at the end of their first year's growth (L_1) are shown in Table 5. The L_1 distributions and means were calculated for each year-class, separately for the spawning areas and years of sampling.

In Table 5 only the means are shown, this being the briefest character to represent the L_1 distribution, although it is not an ideal character as will be pointed out later.

In Table 5 it may be noticed, that differences exist between the spawning areas, and between an individual year-class in successive years on the same spawning ground.

Again the need was felt for statistical tests to establish the reality of the differences. As the L_1 distributions are not normal distributions, but are probably polymodal (Hodgson), no test based on a normal distribution can be used here. We therefore used the X^2-test, being a non-parametric test.

With the help of this test the differences in L_1 distribution between the three spawning areas were analysed for each year-class. The test showed that the differences between Dogger and Channel were highly significant. (For most year-classes $p < 0{\cdot}001$.) The same was found for the differences in L_1 between Dogger and Sandettié, for four out of six year-classes tested, $p \leq 0{\cdot}001$. The differences in the L_1 distributions of the Channel and Sandettié spawners, however, fell well within the possible sampling variation. Yet it may be noticed that for all year-classes the L_1's of the Sandettié spawners is slightly higher than those of the Channel herring.

The variance in the L_1 distributions of the individual year-classes on the same spawning ground was not

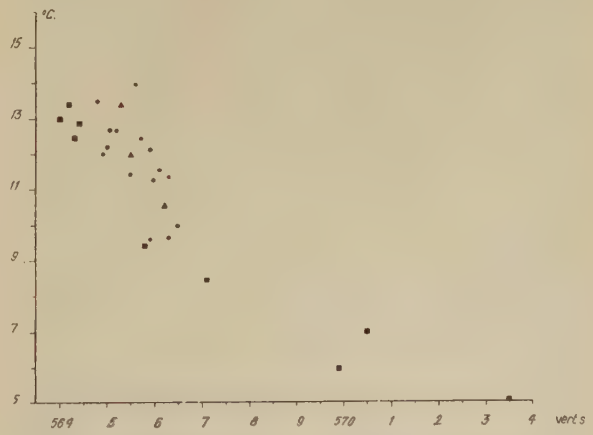


Figure 3. Relationship between mean number of vertebrae and temperature on various spawning grounds (see text). ▪ = data from Le Gall, Runnström, and Wood. ▲ = total 1952, 1953, 1954. • = year-class means.

Table 5

Mean L_1 for Dogger, Sandettié and Channel, calculated per year-class for the three years in which the observations were made

(Between brackets the numbers on which the mean is based. Means based on less than 25 observations have been omitted.)

Year of sampling	Year-class 1951	1950	1949	1948	1947	1946	1945	1944
Dogger								
1952	—	—	12·52 (170)	12·03 (147)	11·40 (59)	11·33 (84)	—	—
1953	—	13·09 (233)	12·16 (208)	12·00 (99)	11·39 (46)	11·17 (167)	12·40 (25)	12·56 (30)
1954	14·20 (274)	13·18 (53)	12·32 (26)	—	—	—	—	—
Total...	14·20 (274)	13·11 (286)	12·32 (404)	12·10 (255)	11·39 (105)	11·31 (262)	12·23 (35)	11·97 (39)
Sandettié								
1953	—	13·09 (119)	10·97 (37)	10·97 (28)	11·97 (25)	10·69 (32)	—	—
1954	12·90 (439)	12·81 (134)	11·09 (30)	—	—	—	—	—
Total...	12·90 (439)	12·94 (253)	11·02 (67)	11·21 (37)	11·60 (35)	10·86 (44)	—	—
Channel								
1952	—	—	11·08 (135)	10·78 (113)	11·56 (129)	10·80 (81)	10·52 (68)	—
1953	—	12·46 (127)	10·77 (113)	10·97 (33)	11·58 (45)	10·91 (26)	10·20 (30)	—
1954	12·72 (138)	12·56 (149)	10·99 (78)	10·36 (45)	11·40 (93)	11·04 (38)	10·02 (30)	—
Total...	12·72 (138)	12·44 (276)	10·95 (326)	10·71 (191)	11·50 (267)	10·88 (145)	10·24 (128)	—

tested for significance, but in view of the results mentioned above they may be expected to be statistically significant.

As for the small variance found on the same spawning ground in the L_1 value of a year-class in the different years of sampling, the test showed only for one case a p as high as 0·02 (Dogger 1949), in a total of 13 cases tested. This is further evidence in support of the assumption that the herring, in general, returns for spawning to the area where it has spawned before. In other words, they are the same herring spawning every year in a certain area. It corroborates the evidence obtained from the age distributions and vertebral counts.

Turning now to the cause of the differences in L_1 distribution between the spawners of the three areas, several authors (for instance, Hodgson, Storrow, and Andersson) have suggested the time of spawning as a possible factor affecting the size of the L_1. In short, fishes having been spawned at different times will in consequence have different actual ages at the moment of the appearance of the first ring on the scale. This means a different period of growth in the time when the L_1 is built up. In this way a difference in the time of spawning might affect the size of the L_1.

In the case of the three spawning grounds Dogger, Sandettié, and Channel the spawning seasons are not the same. On Dogger the spawning time is mainly September—October, in the Sandettié area spawning takes place normally in November, and in the Channel December—January is the main spawning season. As these differences in the time of spawning would be the cause of the differences in the L_1 distributions, Dogger should have the highest L_1 and Channel the lowest. This is exactly what is found, as may be seen in Table 5. However, it must be realized, that this effect of the difference in the time of spawning would only be apparent if the herring in majority spawn in the area where they have hatched.

A difficulty remains, however, in the fact that the L_1 distributions are polymodal. Both Hjort and Hodgson have drawn attention to this fact. They proposed the explanation that the L_1 distributions in the North Sea were combinations of a number of normal distributions and would point to mixing. Hodgson thought he could always distinguish the same three normal curves in the L_1 distributions. The normal distribution with the lowest L_1 mean he expected to belong to herrings hatched in winter in the Sandettié and Channel areas. The largest L_1

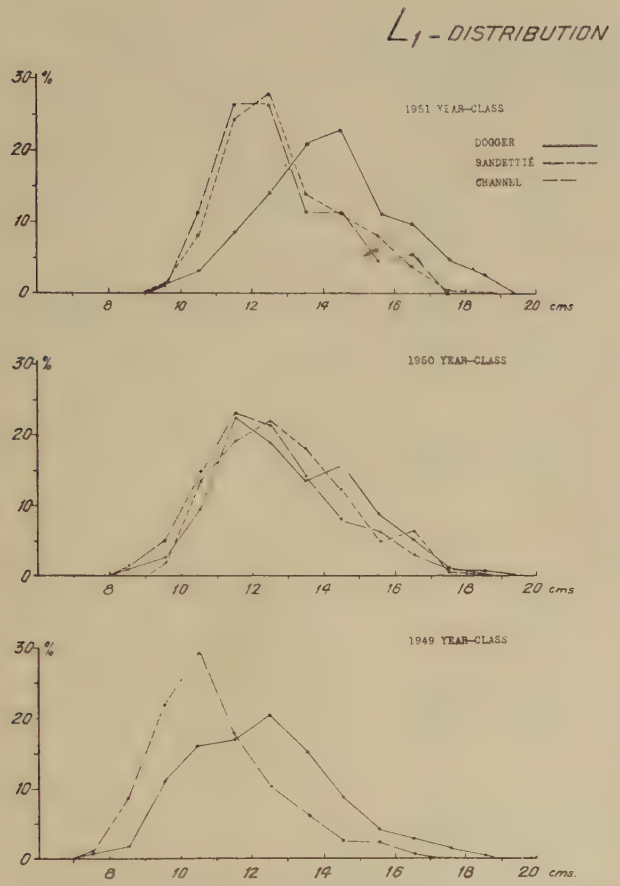


Figure 4. L_1 distributions for the 1951, 1950, and 1949 year-classes of the spawning shoals in the Dogger, Sandettié, and Channel area.

curves would originate from a spawning in summer along the Scottish coast and the intermediate normal curve would contain the offspring of a spawning in the central North Sea (Dogger area) in the autumn. As has been said before, the polymodality may also be noticed in our L_1 distributions. Traces of the 3-curve system of HODGSON may sometimes be detected. This would mean that mixtures of herring originating from several spawning grounds could spawn together, if HODGSON's explanation is right.

Now we found two ways to test HODGSON's hypothesis.

Both make use of HODGSON's assumption, that the largest L_1-group contains animals hatched earlier in the year than those belonging to the smallest L_1 curve.

In the North Sea temperatures are in general decreasing in the latter half of the year, from August till January. Therefore the animals with the largest L_1 will on the average have hatched by higher temperatures than those with a small L_1. In the preceding section we have seen that probably a negative correlation exists between the temperature in the egg stage and the number of vertebrae. For these reasons it might be expected that a negative correlation is found between the L_1 and the vertebral counts, if HODGSON's explanation is right. In Figure 5 the relation between the two characters is shown. As will be seen for none of the three spawning grounds is a negative correlation indicated. On the contrary, for two groups (Dogger and Sandettié) a positive correlation seems apparent.

The other test is based on otolith work, published in this volume by POSTUMA and ZIJLSTRA. In this work hyaline otolith nuclei were found to be different in size for herrings caught in spawning condition in the three spawning areas Dogger, Sandettié, and the Channel.

The otolith nuclei proved to be largest on Dogger, smallest in the Channel, and intermediate in the Sandettié area. This was explained by a difference in the time of spawning, assuming that the transparent centres were built up during the first winter of the life of the herring. In general this comes to the same explanation as the differences in L_1.

Accepting this explanation both the L_1 and the size of the otolith nuclei are supposed to be affected by the time of spawning in the same way. As a consequence a positive correlation between the two characters must be expected, provided that HODGSON's explanation is correct. In Figure 6 the result of this test is shown. As will be seen no positive correlation can be detected in the relation for each spawning ground. However, in case of a mixing of spawners of the three grounds a positive correlation does exist, as a test showed us.

These two arguments both point against HODGSON's explanation concerning the polymodality of the L_1 curves.

How this polymodality is to be explained remains a question. If the time of spawning was the cause of the differences in the L_1 between the three spawning areas, no reason is found why the L_1 distributions should not be normal distributions.

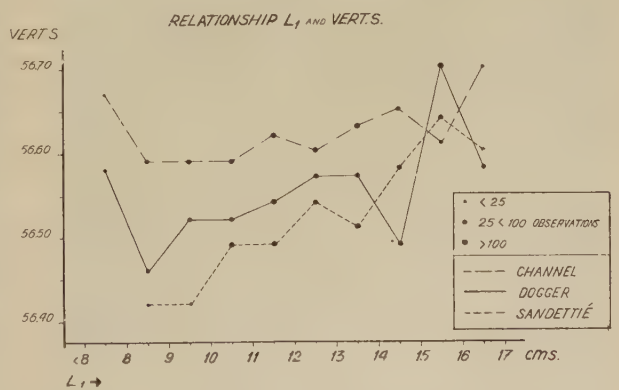


Figure 5. Relationship between L_1 and mean number of vertebrae of Dogger, Sandettié, and Channel spawning herring.

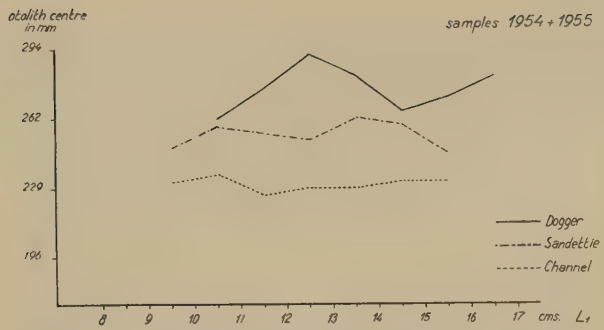


Figure 6. Relationship between L_1 and size of otolith centre for the spawning shoals of Dogger, Sandettié, and Channel.

There might be a solution of this problem in assuming different growth-rates in different parts of the nursery grounds, where the herring grows up in the time before the L_1 is fixed. However, as this has no direct bearing on the problem of the "races" in the North Sea, we will leave the question here.

Growth

The lengths at successive ages of the herring were calculated in the same way as the L_1, viz., from the scale picture and the length of the fish. The data were arranged with regard to year-classes, spawning areas, and year of sampling.

Thus we were able to investigate whether differences existed between the spawning grounds and whether the character "length at a given age" showed variations for a year-class on a certain spawning ground in the different years of sampling.

The mean length per age is shown in Figure 7, for each year-class. From the figure it will be clear that differences do occur between the spawners of the sampled areas. The differences are of about the same magnitude as in the L_1.

At the same time it may be noticed from Figure 7 that the growth of the individual year-classes on all three spawning grounds is different, in that the more recent year-classes show a faster growth-rate. For all three spawning grounds the growth has been accelerated in recent years. This has been observed by several other investigators (Ancellin, Gilis, Cushing).

In order to show the consistency of the character during the three years of this investigation the data for two year-classes (1949 and 1946) are shown in Table 6. Here the $L_{1,2,3}$, etc. are given in three successive years, 1952—1954. Some variation may be noticed in the estimate of the mean length at a certain age for the same year-class. Similar to the treatment of the L_1 data in this respect, the X^2-test was used to see whether the differences could be due to sampling variation.

In total, 17 cases were tested. The test was specially used where an actually measured length distribution

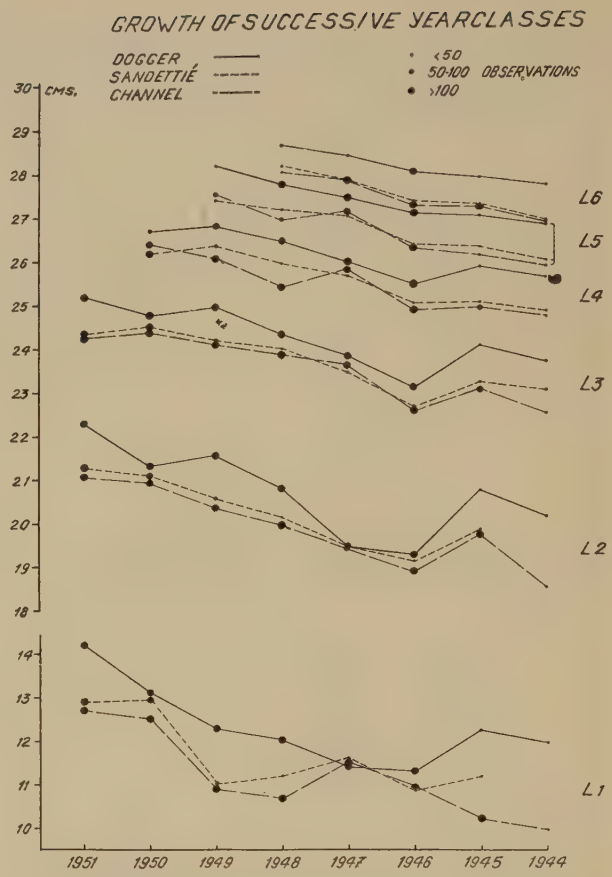


Figure 7. Relationship between age and length (L_1, $_2$, $_3$, etc.) of different year-classes of the spawning herring on the Dogger, Sandettié, and Channel grounds.

could be compared with a calculated one. In none of these cases could significant differences be shown.

Again we have a group of characters showing a great consistency on the same spawning ground, but showing differences on different spawning grounds. Several times already we have mentioned as an obvious explanation of this consistency the hypothesis that the herring in general return every year to the same ground for spawning.

Concerning the cause of the differences between the spawning grounds, we think the original difference in L_1, mentioned in the preceding section, of great importance. This is probably the main cause of the different length distributions found at higher ages. However, there might be something more to it. If the growth curves of the three groups were the same, that means, if the relationship between original length and length increment is the same, one would expect the difference in length to decrease with increasing age (Hodgson).

It is doubtful whether this occurs here. Therefore, it might be that other factors are involved in the

Table 6

Mean $L_{1, 2, 3, etc.}$ for the 1946 and 1949 year-classes in the years 1952—1954 in the spawning areas Dogger Bank, Sandettié, and English Channel

(Means based on less than 25 observations have been omitted.)

Dogger	1949 year-class							
Year	L_1	L_2	L_3	L_4	L_5	L_6	L_7	L_8
1952	12·52	21·89	25·11	—	—	—	—	—
1953	12·16	21·30	24·77	26·74	—	—	—	—
1954	12·32	21·51	25·12	27·08	28·17	—	—	—
Total	12·32	21·56	24·93	26·78	28·17	—	—	—
Channel								
1952	11·08	20·60	24·19	—	—	—	—	—
1953	10·77	20·22	23·87	25·85	—	—	—	—
1954	10·99	20·27	24·34	26·34	27·52	—	—	—
Total	10·94	20·39	24·11	26·05	27·52	—	—	—
Sandettié								
1953	10·97	20·35	24·08	26·12	—	—	—	—
1954	11·09	20·81	24·34	26·61	27·39	—	—	—
Total	11·02	20·56	24·20	26·34	27·39	—	—	—
Dogger	1946 year-class							
1952	11·33	19·15	22·91	25·41	26·98	29·97	—	—
1953	11·17	19·21	23·12	25·46	27·10	28·01	28·68	—
1954	too small numbers							
Total	11·31	19·26	23·09	25·46	27·07	28·08	28·69	—
Channel								
1952	10·80	18·70	22·31	24·81	26·30	27·28	—	—
1953	10·91	18·93	22·61	24·87	26·28	27·26	27·93	—
1954	11·03	19·24	22·75	24·88	26·18	27·15	27·85	28·38
Total	10·94	18·88	22·56	24·84	26·27	27·24	27·88	28·38
Sandettié								
1953	too small numbers							
1954	too small numbers							
Total	10·86	19·10	22·67	24·99	26·35	27·38	27·98	28·84

differences observed between the three spawning areas. We have not investigated this question any further.

Discussion and Conclusions

From the data considered in the preceding section, the following facts can be derived:—

1. Herring shoals visiting the three important spawning areas S.W. Dogger, Sandettié, and Channel, appeared in general to be different in respect of age distribution, vertebral counts, L_1, and growth. Dogger and Channel differed in all four respects, Dogger and Sandettié were different in age distribution, L_1, and probably growth, Channel and Sandettié could be shown to differ in age distribution, vertebral counts, and, possibly, growth. The spawners of the Sandettié area, in general, took up an intermediate position between Dogger and Channel.
2. Characters of herring spawning in three successive years in the same area, proved to be very much alike. This was especially clear for the age distribution and in general length distribution at different ages for the same year-class.

From these observations important suggestions could be made concerning the "racial" structure of the herring group, spawning from July till January in the North Sea and English Channel.

The first observation indicates that the herring shoals, visiting the three spawning areas are not identical. Concerning the cause of the differences found between the three spawning concentrations, the assumption that the majority of the herring return to the area where they have hatched, appeared to provide us with a reasonable explanation. The differences would then be brought about by the environmental inequality of the spawning grounds. The difference in age distribution could be explained by this assumption, although other explanations of the differences may be possible. However, in the case of the differences in the vertebral counts, the explanation seemed to be the only one possible. For the L_1 distributions things were not quite clear, although Hodgson's hypothesis about a mixing of herring originating from different spawning grounds in the spawning shoals, could be rejected. In the paper by Postuma and Zijlstra about the herring otolith, another argument may be found for this "homing" hypothesis.

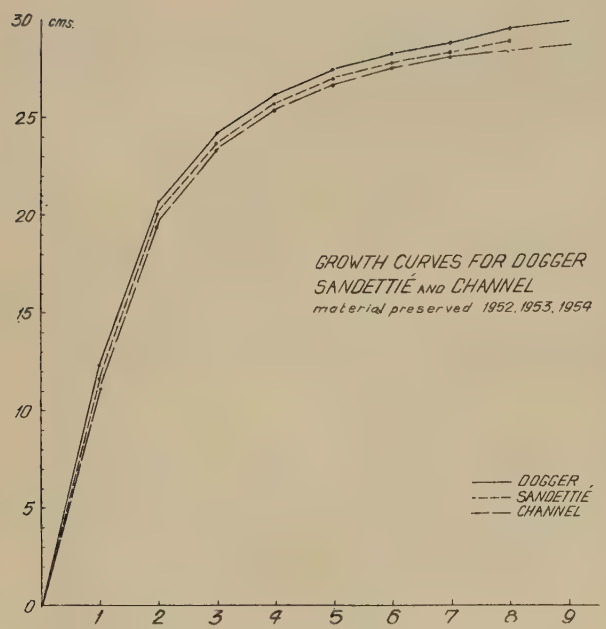


Figure 8. Growth curves of the spawning shoals from the Dogger, Sandettié, and Channel area.

The second observation indicates a returning of the herring for spawning to the area where it has spawned before. This would mean that it is the same adult stock visiting an area every year for spawning.

It was not necessary to assume genetical factors as a cause of the differences in the characters investigated. This does not mean that no genetical differences might exist between the "races". They might, for instance, play a rôle in determining the time of spawning, although it is possible that here too environmental factors are responsible.

Summarizing, the data of this investigation suggest to us that both recruit spawners and older herring tend to spawn in the area where they have hatched originally. Each spawning area would then be used by a separate "spawning community", and interbreeding between the different "spawning communities" would at least be limited.

This suggestion is supported by the fact that every year in the same period herrings spawn in the same distinct and relatively small areas. Several herring fisheries are based on this fact.

If this "homing tendency" is the cause of the existence of herring "races" we might expect each spawning ground to have its own stock. Besides the three stocks dealt with in this paper, many more stocks could be expected to exist, because more spawning grounds are known in the group of the North Sea herring spawning from July till January. The nearer in space and time the spawning takes place the more difficult it will be to distinguish between the "races" due to an increasing similarity of the habitats. At the same time we may allow for the possibility that, if interbreeding occurs, it is likely to be most intensive in adjacent "races". For this reason it will be very difficult to estimate the exactitude of the "homing". With the methods used here this is probably impossible. With tagging of herring in spawning condition in a spawning area and their recapture in spawning condition better results may be obtained.

It seems worthwhile to consider the question if it is correct to attach the term "race" to the groups of herring distinguished here. "Race" always includes an idea of genetical differences. It might be better to use terms such as "populations" or "spawning communities".

A point for consideration in this study is the question how far our data allow for a mixing between the different groups. It must be admitted that a mixing on a small scale will hardly be detectable with the methods used here. Although no calculations have been made it would be expected that slight admixtures of a strange group in a spawning concentration are not noticeable. Evidently, the larger the differences between the stocks the easier it is to detect mixing.

No indications were detected of a shifting of stocks to other spawning areas, as is mentioned by KREFFT *et al.* (1955) as a possibility to explain the decrease in the southern North Sea. KREFFT thinks a displacement of the herring stocks in a northwards direction possible, owing to recent thermic changes in the North Atlantic area. We suggest that such a displacement would have shown in our data, as it had occurred in the years 1952—1955. If this had occurred, the mean L_1, for instance, should have decreased on Dogger for the year-classes involved in the displacement, together with the mean length per age-group. At the same time the age distribution should have changed. There are no signs of such changes.

Summary

Samples of herring caught in spawning condition in the three important spawning areas Dogger Bank, Sandettié, and English Channel were found to differ in respect of age distribution, vertebral counts, and length per age-group. In the same spawning area no differences could be detected in the characters in successive years, indicating that it was the same group returning every year for spawning in an area.

Concerning the cause of the differences in the characters mentioned, a reasonable explanation seemed to be that the herring in general returns to the area where they have hatched. The differences could then be attributed to the environmental inequality of the spawning grounds.

Thus both recruit spawners and older herring spawning on a ground are suggested to originate from spawnings in the same area. Every spawning ground would then be used by its own "spawning community", and the interbreeding between these "communities" would at least be restricted.

Bibliography

Ancellin, J., 1953. "Hareng du Sud de la Mer du Nord et de la Manche Orientale. Campagne de 1952—1953". Cons. Int. Explor. Mer, Ann. Biol., **9**: 202.

Andersson, K. A., 1946. "Some remarks on the fluctuations in the herring fishing on the west coast of Sweden". Rapp. et Proc.-Verb., **118**: 31—39.

Bückmann, A., 1950. "Die Untersuchungen der Biologischen Anstalt über die Ökologie der Heringbrut in der Südlichen Nordsee. Teil II". Helg. Wiss. Meeresunters., **3** (1): 171—205.

Cushing, D. H., 1955. "On the autumn-spawned herring races in the North Sea". J. du Conseil, **21** (1): 44—59.

Dannevig, A., 1950. "The influence of environment in number of vertebrae in plaice". Rep. Norw. Fish. Mar. Invest., **9** (9).

Davis, F. M., 1936. "A contribution to the "Race Question" (Herring)". Rapp. et Proc.-Verb., **100** (2): 12.

Erdmann, W., 1935. "Der deutsche Trawlheringsfang 1934". Der Fischmarkt, N.F., **3** (3): 60—74.

— 1936. "Der deutsche Schleppnetzheringsfang 1935". Ibid., **4** (3): 60—81.

— 1937. "Der deutsche Schleppnetzheringsfang 1936". Ibid., **5** (3): 61—88.

— 1938. "Der deutsche Schleppnetzheringsfang". Ibid., **6** (3): 72—83.

Gabriel, M. L., 1944. "Factors affecting the number and form of vertebrae in *Fundulus heteroclitus*". J. Exp. Zool., **95**: 105—47.

Gilis, C., 1954. "Waarnemingen over de concentraties van de volle haring 1953, de ijle haring 1953—1954 door de Belgische treilers in de Noordzee uitgebaat". Zeewetensch. Inst. Oostende, I.

Heincke, F., 1898. "Naturgeschichte des Herings I". Abh. Deutsch. Seefisch. Verein., **2**: 1—136.

Hjort, J. & E. Lea, 1910. "Some results of the international herring-investigations 1907—1911". Cons. Int. Explor. Mer, Publ. Circ., 61.

Hodgson, W. C., 1936. "The present state of knowledge concerning the origin and distribution of herring populations in western European waters. The Southern Bight". Rapp. et Proc.-Verb., **100** (2): 19.

— 1929. "Investigations into the age, length and maturity of the herring of the southern North Sea". Fish. Invest., **7**: 1—75.

Krefft, G., Schubert K., & Sahrhage, D., 1955. "Der augenblickliche Stand der Erforschung des Nordseeherings mit besonderem Hinblick auf die Frage seiner Überfischung". Arch. f. Fischereiwiss., **6** (3/4): 141—88.

Le Gall, J., 1932. "Statistique biologiques et considérations sur la population harenguière de la Manche Orientale et du Sud de la Mer du Nord (1931)". Revue des Trav., **5** (3): 283.

Le Gall, J., 1933. "Statistique biologiques et considérations sur la population harenguière de la Manche Orientale et du Sud de la Mer du Nord (1932)". Ibid., **6** (2): 125.

— 1934. "Statistique biologiques et considérations sur la population harenguière de la Manche Orientale et du Sud de la Mer du Nord". Ibid., **7** (3): 335.

— 1935. "Statistique biologiques et considérations sur la population harenguière de la Manche Orientale et du Sud de la Mer du Nord, matériel prélevé en 1934". Ibid., **8** (1): 43.

— 1936. "Statistique biologiques et considérations sur la population harenguière de la Manche Orientale et du Sud de la Mer du Nord (matériel prélevé en 1935)". Ibid., **9** (1): 37.

— 1937. "Statistique biologiques et considérations sur la population harenguière de la Manche Orientale et du Sud de la Mer du Nord". Ibid., **10** (1): 33.

Runnström, S., 1941. "Racial analysis of the herring in Norwegian waters". Rep. Norw. Fish. Mar. Invest., **6** (7).

Schmidt, J., 1917. "Racial investigations, II". C. R. Lab. Carlsberg, **14** (1): 11—17.

— 1919. "Racial investigations, III". Ibid., **14** (5): 1—7.

— 1921. "Racial investigations, VII". Ibid., **14** (15): 19—23

Schnackenbeck, W., 1931. "Zum Rassenproblem bei den Fischen". Z. f. Morphol. u. Ökol. d. Tiere, **21** (3/4): 404—566.

— 1936. "The present state of knowledge concerning the origin and distribution of herring populations in western European waters". Rapp. et Proc.-Verb., **100** (2): 28.

Tesch, J. J., 1934. "Herring races in the southern North Sea". Rapp. et Proc.-Verb., **89** (3): 5.

— 1938. "Observations on the herring population in the Flemish Bight and the eastern part of the Channel in the winter 1937—38". Rapp. et Proc.-Verb., **107** (3): 4.

Vedel Tåning, Å., 1944. "Experiments on meristic and other characters in fishes, I". Medd. Komm. Danmarks Fisk.- og Havunders., Ser. Fisk., **11** (3).

— 1952. "Experimental study of meristic characters in fishes". Biol. Rev., **27**: 169—93.

Wood, H., 1936. "Race investigations of the herring population of Scottish waters". Fish. Scotland, Sci. Invest., 1936 (3).

— 1937. "Movements of herring in the northern North Sea". Ibid., 1937 (3).

24.

Recherches sur la Biologie du Hareng

Par Ch. Gilis

Les pêcheurs belges pratiquent deux pêcheries distinctes: aux harengs guais et aux harengs pleins.

A. Harengs Guais

I. Informations préalables

C'est à partir de 1930, que l'Institut d'Etudes Maritimes, Ostende, a entrepris l'étude des harengs vides, appelés "guais" par les Français, "ijle haring" par les Néerlandais, "spent herring" par les Anglais et "Ihlen" ou "abgelaichter Heringe" par les Allemands.

Des concentrations de harengs guais apparaissent chaque hiver de mi-décembre à février, au large des côtes belge et française où elles se déplacent parfois jusque dans les eaux territoriales. Elles y font l'objet d'une exploitation assez importante de la part des chalutiers côtiers et des chalutiers moyens.

Les échantillons d'étude proviennent des pêches commerciales. Ils sont prélevés au hasard au moment du débarquement de la pêche. On applique la méthode des prélèvements fréquents mais d'importance moyenne, soit 50 à 100 harengs par échantillon.

Les harengs sont étudiés aux divers points de vue de la technique usuelle:—

1) Le longueur, 2) le poids, 3) le sexe, 4) la maturité des glandes génitales, 5) la quantité de graisse mésentérique, 6) l'âge, 7) l'allure de la croissance: taille en relation de l'âge et valeur de L_1, 8) le nombre de vertèbres, 9) le nombre d'écailles en carène (K_2) et 10) le contenu stomacal.

L'étude des concentrations s'est poursuivie sans interruption pendant les hivers 1930—31 à 1939—40 et 1941—42 à 1955—56. Au cours de l'hiver 1940—41, la pêche n'a pu avoir lieu par suite des hostilités près de la côte belge.

II. Résultats

Les résultats saisonniers sont répartis d'après les différentes valeurs observées. (Tableaux 1 à 12).

III. Résumé et remarques

1. Longueur (Tableau 1)

Les mensurations sont faites au millimètre, elles montrent que la longueur est comprise entre 18 et 31 cm. Toutefois, les classes de centimètre de < 20 et de > 29 sont rarement représentées dans les échantillons.

La longueur moyenne saisonnière varie entre 238 mm. (1932—33) et 271 mm. (1955—56).

En général, la longueur moyenne est en relation avec la composition des classes d'âge: lorsque les harengs de 3 et 4 ans sont nombreux, la longueur moyenne est basse et dans le cas contraire, elle est élevée. Toutefois, les saisons 1952—53 à 1955—56 font exception: en effet, en dépit d'une représentation anormalement élevée des classes de 3 ans, la longueur moyenne saisonnière est portée à un niveau jamais attaint auparavant. Cette exception indiquerait une croissance plus rapide à partir de 1950.

2. Poids (Tableau 2)

Le poids moyen saisonnier varie entre 86 g. (1930—31) et 127 g. (1955—56). Cette moyenne évolue dans le même sens que la longueur moyenne.

3. Sexe (Tableau 3)

Les écarts entre le nombre des mâles et celui des femelles ne dépassent jamais $100^0/_{00}$, tantôt en faveur des mâles, tantôt en faveur des femelles.

4. Stades de maturité (Tableau 4)

Les harengs guais ayant frayé récemment, leur grande majorité $917^0/_{00}$ à $996^0/_{00}$ présente le stade VIII—II, donc des glandes génitales déjà en régénération.

Tableau 1
Longueur: Fréquence pour 1000 de chaque classe de centimètre

Saisons	Classes de centimètre														Taille moyenne en mm.	Nombre de harengs
	18	19	20	21	22	23	24	25	26	27	28	29	30	31		
1930—31	3	3	33	109	146	120	102	158	217	90	17	2	—	—	241	1,167
1931—32	—	—	—	28	88	161	146	140	213	183	37	4	—	—	251	783
1932—33	—	5	61	117	131	136	162	128	144	90	26	—	—	—	238	1,000
1933—34	1	2	3	15	117	258	199	162	104	95	38	6	—	—	245	1,479
1934—35	—	1	39	100	102	101	210	233	139	50	23	2	—	—	242	1,200
1935—36	1	—	16	75	148	178	142	158	160	88	27	6	1	—	243	1,300
1936—37		—	13	61	74	131	203	187	184	117	24	6	—	—	247	625
1937—38	—	2	16	78	80	89	116	181	228	156	40	14	—	—	250	575
1938—39	—	—	5	28	72	167	162	152	191	150	67	6	—	—	252	600
1939—40	—	—	—	80	80	180	170	220	80	140	50	—	—	—	246	100
1941—42	—	—	4	22	98	129	111	266	236	89	36	9	—	—	248	225
1942—43	—	—	—	2	15	57	149	263	335	135	36	8	—	—	254	525
1943—44	—	—	1	3	36	44	54	224	352	200	73	10	3	—	258	700
1944—45	—	—	7	29	45	49	113	264	322	135	34	2	—	—	252	550
1945—46	—	—	11	30	99	96	81	86	167	304	119	7	—	—	254	700
1946—47	1	2	2	5	56	59	51	106	230	329	142	17	—	—	263	725
1947—48	—	—	3	11	58	73	93	138	219	277	115	13	—	—	260	1,050
1948—49	—	—	1	4	35	50	71	139	227	324	132	16	1	—	264	1,100
1949—50	—	—	8	59	112	75	97	134	159	235	101	20	—	—	256	1,030
1950—51	—	2	4	9	56	156	197	187	171	141	69	7	1	—	254	680
1951—52	—	—	1	3	45	135	177	239	243	127	26	4	—	—	254	950
1952—53	2	2	5	6	40	148	163	130	166	212	111	13	2	—	258	674
1953—54	—	—	1	3	26	112	135	153	153	200	171	43	3	—	270	1,093
1954—55	—	—	—	7	20	103	178	109	112	156	212	91	12	—	265	983
1955—56	—	3	—	4	7	45	89	136	164	172	192	160	25	3	271	755

Tableau 2
Poids: Poids moyen en g.

Saisons	Poids moyen g.
1930—31	86
1931—32	96
1932—33	91
1933—34	97
1934—35	99
1935—36	105
1936—37	109
1937—38	115
1938—39	114
1939—40	103
1941—42	90
1942—43	101
1943—44	108
1944—45	100
1945—46	107
1946—47	113
1947—48	115
1948—49	113
1949—50	100
1950—51	109
1951—52	109
1952—53	115
1953—54	119
1954—55	122
1955—56	127

Tableau 3
Sexe: Fréquence pour 1000 du sexe

Saisons	Sexe ♂	Sexe ♀
1930—31	550	450
1931—32	550	450
1932—33	540	460
1933—34	500	500
1934—35	550	450
1935—36	540	460
1936—37	530	470
1937—38	510	490
1938—39	490	510
1939—40	520	480
1941—42	540	460
1942—43	520	480
1943—44	550	450
1944—45	520	480
1945—46	530	470
1946—47	470	530
1947—48	490	510
1948—49	500	500
1949—50	480	520
1950—51	490	510
1951—52	480	520
1952—53	480	520
1953—54	480	520
1954—55	470	530
1955—56	450	550

Tableau 4
Stades de maturité: Fréquence pour 1000 des stades de maturité

Saisons	Stades de maturité I	II	III	IV	V	VI	VII	VIII—II
1930—31	12	—	3	1	—	1	8	975
1931—32	6	—	—	—	4	12	10	968
1932—33	21	—	—	—	9	2	13	955
1933—34	8	3	—	—	1	7	39	942
1934—35	3	—	—	—	4	5	72	916
1935—36	12	—	—	—	2	—	23	963
1936—37	8	—	—	—	5	16	27	944
1937—38	4	2	—	—	10	17	45	922
1938—39	10	—	—	—	1	7	32	950
1939—40	—	—	—	—	—	—	20	980
1941—42	9	—	—	—	—	9	22	960
1942—43	2	—	—	—	—	6	30	962
1943—44	3	—	—	—	3	1	13	980
1944—45	—	—	—	—	—	2	2	996
1945—46	6	—	—	—	—	1	51	942
1946—47	4	1	—	—	—	4	18	973
1947—48	4	6	—	1	1	4	15	969
1948—49	3	6	—	1	—	2	21	967
1949—50	1	8	—	—	1	1	8	981
1950—51	9	15	—	—	—	—	6	970
1951—52	1	10	—	—	1	6	17	965
1952—53	12	5	—	1	—	5	7	970
1953—54	11	21	—	—	1	30	28	909
1954—55	9	6	—	—	7	6	31	941
1955—56	5	—	—	—	1	4	32	958

5. Graisse mésentérique (Tableau 5)

Les harengs guais sont très pauvres en graisse mésentérique. Les signes 0 et 1 (échelle de Hjort) l'emportent toujours de loin sur les signes + et M. Suivant les saisons, ils totalisent de 833‰ jusque 996‰ des signes observés. L'index de la graisse mésentérique oscille entre 1·41 et 1·93.

6. Age (Tableau 6)

L'âge des harengs est déterminé par l'examen de l'écaille.

Tous nos échantillons sont composés des harengs d'hiver avec l'anneau marginal formé. Pour le calcul de l'âge, il y a donc lieu d'ajouter toujours une année au nombre d'anneaux d'hiver observés.

C'est à partir de l'âge de deux ans (1 anneau d'hiver) que les harengs guais apparaissent dans les pêches commerciales, mais toujours peu nombreux, maximum 10‰ sur tout le lot. Les harengs dépassant l'âge de 10 ans sont moins rares et parfois ils interviennent dans les échantillons avec un chiffre fort élevé: 110‰ en 1946—47; 180‰ en 1947—48; 170‰ en 1948—49 et 146‰ en 1949—50.

Au cours des saisons 1930—31 à 1939—40, les harengs de 3 et 4 ans se montraient généralement les plus nombreux dans les concentrations, tandis que pendant la guerre et jusque la saison 1948—49, les jeunes harengs sont restés déficitaires. A partir de la saison 1949—50, les harengs de 3 et 4 ans dominent

Tableau 5
Graisse mésentérique: Fréquence pour 1000 de la quantité de graisse mésentérique

Saisons	Graisse mésentérique				
	0	1	+	M	Index
1930—31...	485	497	13	5	1·54
1931—32...	—	—	—	—	—
1932—33...	—	—	—	—	—
1933—34...	—	—	—	—	—
1934—35...	256	706	32	6	1·79
1935—36...	146	795	52	7	1·92
1936—37...	203	767	22	8	1·84
1937—38...	108	857	30	5	1·93
1938—39...	197	733	65	5	1·79
1939—40...	280	690	30	—	1·75
1941—42...	484	476	27	13	1·57
1942—43...	588	379	29	4	1·45
1943—44...	623	350	23	4	1·41
1944—45...	503	493	2	2	1·50
1945—46...	280	693	26	1	1·75
1946—47...	516	437	41	6	1·54
1947—48...	340	493	152	15	1·84
1948—49...	499	474	20	7	1·53
1949—50...	340	649	7	4	1·68
1950—51...	187	722	70	21	1·92
1951—52...	144	840	15	1	1·87
1952—53...	190	783	21	6	1·84
1953—54...	155	797	26	22	1·92
1954—55...	200	739	51	10	1·87
1955—56...	124	864	11	1	1·89

Tableau 6
Age: Fréquence pour 1000 de chaque âge observé

Saisons	Age (Ans)										Ecailles lisibles
	2	3	4	5	6	7	8	9	10	+	
1930—31.....	5	228	236	126	150	82	125	34	11	3	1,133
1931—32.....	—	88	229	167	102	141	71	132	44	26	719
1932—33.....	1	252	133	191	120	61	102	43	48	49	955
1933—34.....	5	29	491	87	126	72	32	76	26	56	1,445
1934—35.....	—	250	57	409	67	81	55	24	34	23	1,178
1935—36.....	—	268	280	31	239	37	60	28	18	39	1,291
1936—37.....	—	152	298	170	19	210	45	52	20	34	618
1937—38.....	4	265	118	184	117	23	186	23	40	40	570
1938—39.....	—	82	389	95	137	108	14	125	7	43	576
1939—40.....	—	160	220	300	70	100	80	10	60	—	100
1941—42.....	9	227	107	328	138	107	49	13	9	13	225
1942—43.....	—	33	264	97	303	136	114	31	14	8	515
1943—44.....	—	95	32	178	88	311	142	112	21	21	697
1944—45.....	2	98	107	16	194	76	307	116	64	20	548
1945—46.....	1	241	128	72	27	165	57	188	74	47	698
1946—47.....	7	99	121	73	81	34	212	63	200	110	700
1947—48.....	—	115	95	167	88	79	40	180	55	181	694
1948—49.....	2	94	115	59	164	98	95	70	135	168	939
1949—50.....	—	184	195	75	46	124	88	72	70	146	614
1950—51.....	—	174	222	187	84	65	103	60	43	62	369
1951—52.....	4	197	266	237	140	65	33	38	4	16	493
1952—53.....	12	372	124	153	120	95	46	24	30	24	589
1953—54.....	5	276	216	125	119	121	80	25	16	17	804
1954—55.....	5	261	210	129	90	92	103	61	23	26	819
1955—56.....	3	189	244	182	102	72	73	76	41	18	683

Tableau 7
Allure de croissance: Longueur moyenne en mm. par rapport à l'âge

Saisons	Age (Ans)									Classes d'âge de:
	2	3	4	5	6	7	8	9	10	
1930—31	186	215	229	249	254	262	263	265	270	1928 à 1920
1931—32	—	220	233	241	257	260	267	268	268	1929 à 1921
1932—33	210	211	226	237	245	256	260	266	265	1930 à 1922
1933—34	206	222	234	243	251	257	264	268	273	1931 à 1923
1934—35	—	217	233	247	255	258	261	269	270	1932 à 1924
1935—36	—	217	236	250	257	262	265	270	273	1933 à 1925
1936—37	—	219	238	249	259	262	266	269	265	1934 à 1926
1937—38	200	223	242	256	259	265	268	272	271	1935 à 1927
1938—39	—	223	237	253	263	265	275	—	—	1936 à 1928
1939—40	—	224	237	250	266	269	270	—	—	1937 à 1929
1941—42	—	235	248	254	261	266	268	—	—	1939 à 1931
1942—43	—	226	249	258	259	266	269	—	—	1940 à 1932
1943—44	—	234	249	257	267	264	270	—	—	1941 à 1933
1944—45	—	228	239	255	256	264	264	—	—	1942 à 1934
1945—46	—	229	248	260	266	264	273	—	—	1943 à 1935
1946—47	—	228	246	257	265	273	—	—	—	1944 à 1936
1947—48	—	231	248	256	265	270	273	273	275	1945 à 1937
1948—49	—	233	249	255	264	267	273	276	275	1946 à 1938
1949—50	—	223	246	254	266	268	272	277	277	1947 à 1939
1950—51	—	236	245	257	264	269	274	277	278	1948 à 1940
1951—52	216	235	251	260	265	270	276	274	277	1949 à 1941
1952—53	207	239	255	268	271	276	279	281	280	1950 à 1942
1953—54	229	240	261	270	277	280	283	286	287	1951 à 1943
1954—55	232	242	261	276	281	286	286	290	287	1952 à 1944
1955—56	205	246	262	275	283	288	290	291	294	1953 à 1945

Tableau 8
Allure de croissance: Valeur moyenne de L_1 en mm. pour chaque âge

Saisons	Age (Ans)								
	2	3	4	5	6	7	8	9	10
1946—47	—	109	110	109	117	118	117	120	108
1947—48	—	—	—	—	—	—	—	—	—
1948—49	—	105	107	105	107	104	114	115	108
1949—50	—	110	107	104	106	105	112	111	111
1950—51	—	115	105	104	101	100	103	112	113
1951—52	126	100	105	103	95	93	108	100	106
1952—53	126	109	110	112	103	101	101	101	105
1953—54	153	116	105	106	113	105	105	99	97
1954—55	163	124	120	111	110	115	109	107	107
1955—56	122	135	126	122	107	108	113	111	110

à nouveau mais dans une mesure beaucoup plus accentuée qu'avant la guerre.

Au cours des 25 années d'observations, 11 générations se sont montrées très abondantes, à savoir: 1927, 1929, 1931, 1932, 1934, 1938, 1946, 1947, 1949, 1950 et 1951; 6, assez abondantes: 1933, 1935, 1937, 1942, 1945 et 1948; 8, plutôt mauvaises: 1928, 1930, 1936, 1939, 1940, 1941, 1943 et 1944.

7. Allure de croissance

(a) Longueur moyenne par rapport à l'âge (Tableau 7).

Jusqu'en 1950—51, on ne constate guère des grands écarts entre la taille moyenne des harengs par rapport à leur âge, tandis qu'à partir de 1951—52, on observe une nette et constante augmentation de cette moyenne.

(b) Valeur de L_1 (Tableau 8).

La valeur moyenne de L_1 des classes 1949 à 1952 s'avère également sensiblement supérieure à celle observée pour les classes antérieures.

8. Nombre de vertèbres (Tableaux 9 et 10)

Le nombre de vertèbres observées par épine dorsale oscille entre 52 et 61. Toutefois, les nombres 52, 53, 60 et 61 se rencontrent rarement. On note une prédominance énorme des individus à 56 et 57 vertèbres, ainsi qu'une forte prédominance de 57 sur 56.

Selon les saisons 8‰ à 36‰ des épines dorsales montrent une ou plusieurs vertèbres soudées, mais dans les calculs il est fait abstraction de ces dernières.

Tableau 9
Vertèbres: Fréquence pour 1000 du nombre de vertèbres

Saisons	Nombre de vertèbres										Nombre de harengs	Moyenne vertébrale	Déviation Standard	Fluctuation probable de la moyenne	Soudures[1])
	52	53	54	55	56	57	58	59	60	61					
1930—31...	—	—	—	14	363	555	63	5	—	—	1,167	56·69	0·637	0·063	?
1931—32...	—	—	—	17	363	549	69	2	—	—	783	56·68	0·637	0·077	?
1932—33...	—	1	2	31	419	498	48	—	1	—	1,000	56·56	0·664	0·061	?
1933—34...	1	—	3	20	435	478	61	2	—	—	1,479	56·57	0·672	0·059	?
1934—35...	—	—	—	25	430	483	60	2	—	—	1,200	56·58	0·650	0·063	?
1935—36...	—	—	1	25	471	472	30	1	—	—	1,300	56·51	0·612	0·057	?
1936—37...	—	—	—	27	472	456	45	—	—	—	625	56·52	0·627	0·085	?
1937—38...	—	—	2	42	441	473	40	2	—	—	575	56·51	0·660	0·093	?
1938—39...	—	—	6	52	423	482	37	—	—	—	600	56·49	0·680	0·094	?
1939—40...	—	—	—	50	350	550	50	—	—	—	100	56·60	0·664	0·224	?
1941—42...	—	—	—	71	400	440	84	5	—	—	225	56·55	0·766	0·172	?
1942—43...	—	—	—	21	448	478	53	—	—	—	525	56·60	0·652	0·096	?
1943—44...	—	—	—	41	462	444	53	—	—	—	700	56·51	0·662	0·084	?
1944—45...	—	—	—	45	396	504	55	—	—	—	550	56·57	0·668	0·096	?
1945—46...	—	—	1	26	387	514	71	1	—	—	700	56·63	0·662	0·084	?
1946—47...	—	—	3	25	418	482	70	1	—	1	725	56·60	0·690	0·086	?
1947—48...	—	—	2	45	405	492	55	1	—	—	1,050	56·56	0·684	0·071	?
1948—49...	—	—	4	53	395	465	80	3	—	—	1,100	56·57	0·742	0·075	?
1949—50...	—	—	1	24	401	514	58	2	—	—	992	56·61	0·648	0·069	34
1950—51...	—	—	—	26	426	485	60	3	—	—	662	56·59	0·659	0·086	22
1951—52...	—	—	1	41	398	508	52	—	—	—	918	56·57	0·662	0·072	32
1952—53...	2	—	3	26	408	491	68	2	—	—	661	56·59	0·705	0·093	8
1953—54...	—	—	1	22	450	474	50	3	—	—	1,043	56·56	0·645	0·066	25
1954—55...	—	—	—	23	419	507	50	—	1	—	947	56·59	0·634	0·070	36
1955—56...	—	—	1	29	376	525	69	—	—	—	728	56·63	0·659	0·082	28

[1]) ‰ des colonnes avec vertèbres soudées

La moyenne saisonnière des vertèbres oscille entre 56·69 (1930—31) et 56·49 (1938—39), soit un écart de deux dixièmes de vertèbres pour l'ensemble des 25 saisons envisagées.

Tableau 10
Vertèbres : Répartition de la moyenne vertébrale d'après les mois

Saisons	Décembre	Janvier	Février	Mars
1931—32.....	56·65	56·71	56·65	—
1932—33.....	56·48	56·65	—	—
1933—34.....	56·51	56·60	56·63	—
1934—35.....	56·58	56·60	56·60	—
1935—36.....	56·48	56·54	56·49	—
1936—37.....	56·48	56·57	56·51	—
1937—38.....	56·53	56·52	—	—
1938—39.....	56·49	56·51	—	—
1943—44.....	56·35	56·58	56·63	—
1944—45.....	56·43	56·62	56·71	—
1945—46.....	56·53	56·67	56·63	56·59
1946—47.....	56·51	56·67	56·65	—
1947—48.....	56·44	56·54	56·65	—
1948—49.....	56·56	56·58	56·58	—
1949—50.....	56·56	56·64	56·63	—
1950—51.....	56·60	56·58	—	—
1951—52.....	56·63	56·52	56·58	—
1952—53.....	56·53	56·66	—	—
1953—54.....	56·53	56·60	56·56	—
1954—55.....	56·58	56·60	56·60	—
1955—56.....	56·62	56·66	56·59	—

Si au lieu de considérer la moyenne vertébrale saisonnière, on prend à part chacun des mois séparément, on constate une hausse assez sensible à partir de janvier. Cette hausse pourrait bien signifier une pénétration de harengs de la Manche orientale dans l'extrême sud de la Mer du Nord.

9. Nombre d'écailles en carène, K_2 (Tableau 11)

C'est seulement à partir de la saison 1946—47 que le nombre de K_2 a été pris en considération, à la suite des recommandations formulées lors de la réunion spéciale des experts du hareng à Aberdeen en 1946.

Le nombre de K_2 varie entre 12 et 20. Les nombres extrêmes, soit 12, 13, 18 à 20, y sont rarement représentés. Les individus possédant 14 et 15 K_2 jouent le rôle principal dans la constitution du stock.

La moyenne saisonnière de K_2 est comprise entre 14·62 (1947—48) et 14·87 (1953—54).

10. Contenu stomacal (Tableau 12)

Au début de la campagne aux harengs guais tous les estomacs sont pour ainsi dire vides. Vers la fin de la campagne l'on observe de la nourriture, constituée le plus souvent par des débris de copépodes et moins souvent par des débris de schizopodes, œufs de hareng et très rarement par quelques larves de crustacés et de poissons. Par ailleurs, dès que les harengs commencent à se nourrir, ils se dispersent, ce qui signifie la fin prochaine de la pêche aux harengs guais.

Tableau 11
Ecailles en carène (K_2): Fréquence pour 1000 du nombre d'écailles en carène

Saisons	Nombre d'écailles en carène									Nombre de harengs	Moyenne	Déviation Standard	Fluctuation probable de la moyenne
	12	13	14	15	16	17	18	19	20				
1946—47.....	—	53	291	509	139	8	—	—	—	375	14·76	0·786	0·137
1947—48.....	1	79	340	455	114	10	1	—	—	1,050	14·63	0·831	0·087
1948—49.....	—	50	335	463	141	10	1	—	—	1,100	14·73	0·808	0·082
1949—50.....	1	32	294	493	156	23	—	1	—	1,019	14·84	0·819	0·086
1950—51.....	—	33	298	493	159	16	1	—	—	678	14·83	0·796	0·103
1951—52.....	—	53	323	475	138	7	—	3	1	950	14·72	0·835	0·091
1952—53.....	—	—	—	—	—	—	—	—	—	—	—	—	—
1953—54.....	2	48	271	481	161	33	4	—	—	983	14·87	0·884	0·095
1954—55.....	1	40	291	472	173	19	4	—	—	978	14·85	0·850	0·092
1955—56.....	—	39	313	480	153	15	—	—	—	747	14·79	0·799	0·099

Tableau 12
Contenu stomacal: Fréquence pour 1000 des estomacs avec contenu

Saisons	Estomacs avec contenu	Saisons	Estomacs avec contenu	Saisons	Estomacs avec contenu
1930—31.....	?	1939—40.....	0	1948—49.....	31
1931—32.....	?	1941—42.....	133	1949—50.....	3
1932—33.....	?	1942—43.....	36	1950—51.....	4
1933—34.....	?	1943—44.....	11	1951—52.....	8
1934—35.....	99	1944—45.....	0	1952—53.....	100
1935—36.....	66	1945—46.....	17	1953—54.....	100
1936—37.....	53	1946—47.....	112	1954—55.....	0
1937—38.....	106	1947—48.....	10	1955—56.....	42
1938—39.....	15				

B. Harengs Pleins

I. Informations préalables

L'étude des concentrations des harengs, dits "pleins" a débuté en 1946; elle s'est poursuivie sans interruption jusqu'en 1955.

D'après son origine, le matériel d'étude est réparti en trois régions: la région septentrionale, la région centrale et la région méridionale de la Mer du Nord.

Dans la région septentrionale, les échantillons sont récoltés principalement pendant les mois de juillet et d'août au Bressay Bank et au Fladen; dans la région centrale, pendant les mois de septembre et d'octobre, au Turbot Bank, Long Forties, Old Devil's Hole, Eastern Hole, Gut, Bruceys Garden, Dogger Bank et Skate Hole; dans la région méridionale, pendant les mois de novembre et de décembre, dans une zone assez restreinte comprise entre les bateaux-phares "West-Hinder", "Ruytingen", "Sandettié" et "East Goodwin".

Prélevés au hasard par le patron du chalutier au moment du déversement de la pêche sur le pont, les échantillons sont placés dans un récipient et conservé dans la cale aux poissons, jusqu'au moment du retour au port. Le patron fournit les renseignements concernant la date et le lieu de la pêche, le nombre d'heures de pêche, l'importance de la pêche, la force motrice, etc.

Pour l'étude des harengs pleins, on applique aussi la méthode des prélèvements fréquents dont l'importance varie de 50 à 100 harengs.

Les méthodes d'analyses et les valeurs observées sont identiques à celles des harengs guais.

II. Résultats

Comme pour le hareng guais, les résultats sont répartis d'après les différentes valeurs observées (Tableaux 13 à 24).

III. Résumé et remarques

1. Longueur (Tableau 13)

Les harengs sont mesurés au millimètre inférieur. La longueur des harengs pleins varie de 19 à 31 cm. Les tailles extrêmes, soit 19, 20 et 31 cm. s'observent très rarement.

Les tailles moyennes des harengs pleins sont sujettés à d'assez grandes fluctuations saisonnières: dans la région septentrionale, elles varient de 263 mm. (1947) à 287 mm. (1952); dans la région centrale, de 260 mm. (1950) à 277 mm. (1955) et dans la région méridionale, de 258 mm. (1954) à 268 mm. (1955).

La longueur moyenne est donc sensiblement plus élevée dans la région septentrionale que dans les deux

Tableau 13
Longueur: Fréquence pour 1000 de chaque classe de centimètre

Années	Classes de centimètre													Taille moyenne en mm.	Nombre de harengs
	19	20	21	22	23	24	25	26	27	28	29	30	31		
Région septentrionale															
1946.....	—	—	10	—	13	45	113	332	304	138	38	7	—	286	398
1947.....	—	—	—	14	34	124	202	260	230	102	30	4	—	263	500
1948.....	—	—	—	5	—	5	63	168	407	283	67	2	—	273	400
1949.....	—	—	—	2	10	17	59	155	302	342	100	13	—	276	690
1950.....	—	—	—	29	61	160	160	204	171	182	29	4	—	263	280
1951.....	—	—	—	—	3	18	112	192	220	297	115	40	3	276	400
1952.....	—	—	—	—	—	—	10	45	200	305	310	115	15	287	200
1953.....	—	—	3	3	38	52	96	90	200	159	255	83	21	278	290
1954.....	—	8	28	38	72	102	162	150	170	108	102	60	—	265	400
1955.....	(pas d'observations)														
Région centrale															
1946.....	—	4	41	41	12	41	135	268	322	112	20	4	—	264	245
1947.....	—	—	4	6	38	58	134	230	308	170	48	4	—	272	500
1948.....	—	—	—	12	28	25	90	205	345	229	63	—	3	271	600
1949.....	—	—	11	32	89	105	117	146	289	171	38	2	—	264	630
1950.....	—	—	—	25	110	186	193	150	149	151	35	1	—	260	920
1951.....	2	3	3	9	64	110	248	267	182	70	37	3	2	261	644
1952.....	—	1	2	16	98	137	140	166	200	172	64	4	—	264	900
1953.....	—	—	3	21	67	116	132	165	179	184	104	27	2	267	1,045
1954.....	2	7	17	25	79	103	144	153	127	148	132	63	—	267	798
1955.....	—	—	3	6	46	95	132	97	95	123	235	140	28	277	635
Région méridionale	(de 1946 à 1952 pas d'observations)														
1953.....	—	—	5	15	69	129	134	213	257	139	39	—	—	264	202
1954.....	—	—	4	47	150	228	158	102	106	146	47	12	—	258	254
1955.....	—	—	—	5	68	122	159	180	145	173	114	32	2	268	560

régions plus méridionales. Il est possible que cette différence soit due, pour une grande part, à la présence hypothétique d'une certaine proportion de Harengs de Printemps dans les concentrations de la région septentrionale.

2. Poids (Tableau 14)

Dans la région septentrionale, le poids moyen saisonnier varie de 153 g. à 210 g.; dans la région centrale, de 142 g. à 185 g. et dans la région méridionale, de 137 g. à 158 g.

La régression du poids moyen constatée dans la région centrale et celle plus accentuée encore dans la région méridionale sont pour la plus grande part, imputable à l'apparition dans les concentrations d'une proportion de plus en plus grande de harengs guais (stades VII et VIII—II).

3. Sexe (Tableau 15)

Pour l'ensemble des saisons considérées, la proportion des mâles l'emporte sur celle des femelles. Cette prédominance est plus sensible dans la région septentrionale que dans la région centrale, tandis que dans la région méridionale les proportions des deux sexes s'équilibrent plus ou moins.

4. Stades de maturité (Tableau 16)

Dans les régions septentrionale et centrale, tous les stades de maturité sont représentés, alors que dans la région méridionale, les stades III et IV font défaut. La maturité progresse de région à région à mesure que les concentrations descendent vers le sud. Aussi, dans la région septentrionale, les stades III à V se montrent les plus fréquents; dans la région centrale, les stades IV à VI et dans la région méridionale, les stades V à VIII—II.

Ces constatations indiquent que dans la région septentrionale (juillet et août) on a à faire à des concentrations de prématuration et dans les régions plus méridionales (septembre à décembre), à des concentrations de reproduction.

5. Graisse mésentérique (Tableau 17)

Les harengs provenant de la région septentrionale sont très riches en graisse mésentérique (index: 2·17 à 3·47), ceux de la région centrale en sont beaucoup moins fournis (index: 1·67 à 2·24), tandis que ceux de la région méridionale n'en possèdent que très peu (index: 1·41 à 1·72).

Ces résultats montrent que les harengs à gonades peu développées possèdent plus de graisse que ceux à

Tableau 14
Poids: Poids moyen en g.

Années	Régions		
	Septentrionale	Centrale	Méridionale
	Poids moyen en g.		
1946.....	156	144	?
1947.....	153	156	?
1948.....	165	151	?
1949.....	165	142	?
1950.....	164	153	?
1951.....	179	151	?
1952.....	210	161	?
1953.....	208	170	156
1954.....	170	162	137
1955.....	?	185	158

Tableau 15
Sexe: Fréquence pour 1000 du sexe

Années	Régions					
	Septentrionale		Centrale		Méridionale	
	♂	♀	♂	♀	♂	♀
1946.....	545	455	474	526	?	?
1947.....	570	430	540	460	?	?
1948.....	537	463	517	483	?	?
1949.....	555	445	520	480	?	?
1950.....	521	479	499	501	?	?
1951.....	520	480	480	520	?	?
1952.....	640	360	498	502	?	?
1953.....	434	566	483	517	673	327
1954.....	495	505	504	496	496	504
1955.....	?	?	498	502	457	543

Tableau 16
Stades de maturité: Fréquence pour 1000 des stades de maturité

Années	Stades de maturité							
	I	II	III	IV	V	VI	VII	VIII–II
Région septentrionale								
1946.....	13	18	93	228	580	43	10	15
1947.....	56	120	128	302	384	2	—	8
1948.....	5	48	108	235	492	50	30	32
1949.....	1	12	61	164	543	203	7	9
1950.....	14	18	379	346	239	—	4	—
1951.....	40	28	277	387	268	—	—	—
1952.....	25	35	105	325	510	–	–	—
1953.....	21	17	65	314	459	10	7	107
1954.....	45	15	212	418	305	—	—	5
1955.....	(pas d'observations)							
Région centrale								
1946.....	29	4	61	127	608	139	24	8
1947.....	38	78	22	92	502	130	6	132
1948.....	8	22	97	88	257	353	42	133
1949.....	2	11	13	37	162	675	41	59
1950.....	2	4	58	140	421	296	21	58
1951.....	22	34	59	231	368	168	—	118
1952.....	27	24	66	148	383	293	9	50
1953.....	13	25	42	119	500	211	14	76
1954.....	60	35	25	99	405	263	35	78
1955.....	5	57	35	74	423	345	8	53
Région méridionale								
1953.....	5	10	—	—	450	292	208	35
1954.....	12	12	—	—	268	464	35	209
1955.....	2	3	—	2	429	453	29	82
de 1946 à 1952 pas d'observations								

Tableau 17
Graisse mésentérique: Fréquence pour 1000 de la quantité de graisse mésentérique

Années	Graisse mésentérique				
	0	1	+	M	Index
Région septentrionale					
1946.....	271	387	239	103	2·17
1947.....	46	310	408	236	2·83
1948.....	235	355	230	180	2·36
1949.....	236	497	103	164	2·20
1950.....	7	289	322	382	3·08
1951.....	35	245	385	335	3·12
1952.....	150	370	280	200	2·53
1953.....	172	372	352	104	2·39
1954.....	50	240	348	362	3·47
1955.....	(pas d'observations)				
Région centrale					
1946.....	469	323	114	94	1·83
1947.....	228	508	142	122	2·16
1948.....	317	418	123	142	2·09
1949.....	461	456	35	48	1·67
1950.....	309	401	185	105	2·09
1951.....	238	394	259	109	2·24
1952.....	246	400	230	124	2·23
1953.....	313	420	213	54	2·01
1954.....	233	490	174	103	2·15
1955.....	258	547	142	53	1·98
Région méridionale					
1953.....	623	357	10	10	1·41
1954.....	358	610	24	8	1·68
1955.....	305	682	13	—	1·72
de 1946 à 1952 pas d'observations					

gonades mûres, de sorte que la maturation va de pair avec une diminution de la graisse mésentérique.

6. Age (Tableau 18)

A partir de l'âge de trois ans, les harengs pleins apparaissent dans les pêches commerciales. Les harengs âgés de plus de 10 ans sont relativement nombreux dans les régions septentrionale et centrale (21 à 210‰) et peu nombreux, dans la région méridionale (6 à 20‰).

Au cours des dix années d'observation, 5 classes d'âge ont été annotées comme constituant de très bonnes classes: 1946, 1949, 1950, 1951 et 1952; deux classes considérées comme assez bonnes: 1945 et 1947 et trois classes considérées comme étant médiocres: 1943, 1944 et 1948.

Tableau 18
Age: Fréquence pour 1000 de chaque âge observé

Années	Age (Ans) 2	3	4	5	6	7	8	9	10	+	Ecailles lisibles
Région septentrionale											
1946	—	22	68	112	242	155	118	134	96	53	322
1947	—	64	139	238	169	139	70	76	35	70	172
1948	—	6	127	91	212	146	206	115	24	73	165
1949	—	11	34	113	128	185	208	192	91	38	265
1950	—	155	330	82	62	82	144	72	52	21	97
1951	—	24	106	200	200	153	94	70	82	71	85
1952	—	9	67	84	151	126	151	84	118	210	119
1953	—	91	210	124	120	139	57	91	72	96	209
1954	46	235	267	129	64	83	74	51	23	28	217
1955	(pas d'observations)										
Région centrale											
1946	18	90	144	132	246	126	90	78	36	40	167
1947	—	42	42	90	125	250	152	160	42	97	144
1948	—	24	219	98	130	163	114	73	73	106	123
1949	—	80	151	132	100	199	79	135	64	60	251
1950	—	82	263	181	82	91	82	73	70	76	328
1951	—	40	196	365	169	54	34	68	40	34	148
1952	—	183	169	149	215	126	38	34	41	45	443
1953	6	221	247	124	83	139	67	24	33	56	675
1954	14	140	261	166	88	68	96	39	27	101	487
1955	—	181	194	80	117	73	69	120	37	129	464
Région méridionale											
1953	—	230	267	143	87	137	93	12	25	6	161
1954	10	446	270	64	73	44	39	10	24	20	204
1955	—	230	275	167	123	78	53	36	29	9	448
de 1946 à 1952 pas d'observations											

Tableau 19
Allure de la croissance: Longueur moyenne en mm. par rapport à l'âge

Années	Age (Ans) 2	3	4	5	6	7	8	9	10	Classes d'âge de:
Région septentrionale										
1946	—	229	250	261	269	275	271	274	276	1943 à 1936
1947	—	240	248	259	266	270	280	275	280	1944 à 1937
1948	—	249	270	266	271	277	275	279	284	1945 à 1938
1949	—	236	254	269	270	276	280	283	284	1946 à 1939
1950	—	237	247	252	261	275	277	279	279	1947 à 1940
1951	—	239	263	268	272	280	286	281	285	1948 à 1941
1952	—	265	274	278	280	285	289	293	293	1949 à 1942
1953	—	241	257	274	287	284	287	292	293	1950 à 1943
1954	216	237	260	277	281	288	292	294	298	1952 à 1944
1955	(pas d'observations)									
Région centrale										
1946	—	223	253	266	269	275	273	274	267	1943 à 1936
1947	—	244	250	267	264	273	273	278	272	1944 à 1937
1948	—	237	265	270	273	274	276	277	278	1945 à 1938
1949	—	233	249	261	267	273	275	279	282	1946 à 1939
1950	—	239	250	260	268	273	280	283	284	1947 à 1940
1951	—	243	258	265	272	276	276	276	285	1948 à 1941
1952	—	245	259	271	276	282	287	288	288	1949 à 1942
1953	231	242	262	271	276	283	287	287	293	1950 à 1943
1954	218	245	262	276	283	287	290	297	300	1952 à 1944
1955	—	249	264	279	289	294	295	297	302	1952 à 1945
Région méridionale										
1953	—	244	262	270	278	279	282	276	288	1950 à 1943
1954	219	241	257	272	284	289	283	288	295	1952 à 1944
1955	—	245	261	275	285	289	292	292	296	1952 à 1945
de 1946 à 1952 pas d'observations										

Tableau 20
Allure de la croissance: Valeur moyenne de L_1 en mm. pour chaque âge

Années	Age (Ans)								
	2	3	4	5	6	7	8	9	10
Région septentionale									
1946.....	—	119	118	122	120	129	114	113	107
1949.....	—	133	109	113	115	115	118	119	120
1950.....	—	115	105	121	99	119	114	112	114
1951.....	—	100	110	114	108	114	133	112	115
1952.....	—	111	125	113	111	118	125	124	123
1953.....	—	114	108	114	120	115	116	124	119
1954.....	158	120	108	105	113	111	108	100	128
en 1947, 1948 et 1955 pas d'observations									
Région centrale									
1946.....	—	112	119	123	119	130	119	108	103
1949.....	—	123	109	109	113	113	112	115	118
1950.....	—	111	106	108	111	114	105	115	103
1951.....	—	119	116	108	112	101	108	107	110
1952.....	—	114	111	117	108	113	114	107	125
1953.....	128	120	114	107	112	118	110	119	104
1954.....	151	123	113	115	114	112	112	121	124
1955.....	—	139	122	120	119	121	119	115	118
en 1947 et 1948 pas d'observations									
Région méridionale									
1953.....	—	120	108	100	107	103	101	106	108
1954.....	149	127	119	107	116	123	109	109	117
1955.....	—	136	126	125	115	109	118	114	116
de 1946 à 1952 pas d'observations									

Tableau 21
Vertèbres: Fréquence pour 1000 du nombre de vertèbres

Années	Nombre de vertèbres								Nombre de harengs	Moyenne vertébrale	Déviation Standard	Fluctuation probable de la moyenne	Soudures[1])
	52	53	54	55	56	57	58	59					
Région septentrionale													
1946.....	—	—	7	60	435	448	50	- -	398	56·47	0·714	0·121	?
1947.....	—	—	4	50	438	442	60	6	500	56·52	0·728	0·110	?
1948.....	—	—	5	20	455	423	95	2	400	56·59	0·717	0·121	?
1949.....	—	—	—	25	468	453	50	4	678	56·54	0·650	0·084	17
1950.....	—	—	—	36	451	495	18	—	275	56·49	0·598	0·122	18
1951.....	—	—	—	23	419	477	79	2	394	56·62	0·735	0·125	15
1952.....	5	—	—	48	505	399	43	- -	188	56·42	0·726	0·179	41
1953.....	—	—	4	92	422	386	85	11	282	56·49	0·833	0·167	11
1954.....	—	2	2	56	423	466	51	—	395	56·50	0·706	0·120	13
1955.....	(pas d'observations)												
Région centrale													
1946.....	—	—	4	33	522	388	53	—	245	56·45	0·667	0·187	?
1947.....	—	—	2	40	442	456	60	—	500	56·53	0·668	0·101	?
1948.....	—	—	3	52	363	524	55	3	600	56·59	0·702	0·097	?
1949.....	—	—	—	34	455	464	45	2	617	56·53	0·647	0·088	21
1950.....	—	—	—	41	463	453	41	2	889	56·50	0·653	0·074	30
1951.....	—	—	—	58	412	490	40	—	623	56·51	0·668	0·090	33
1952.....	—	—	1	45	436	448	65	5	864	56·54	0·709	0·081	26
1953.....	—	—	5	56	456	404	76	3	1,025	56·50	0·750	0·079	7
1954.....	—	—	9	52	405	483	50	1	768	56·52	0·718	0·087	35
1955.....	—	—	3	28	480	434	55	—	617	56·51	0·673	0·091	25
Région méridionale													
1953.....	—	—	10	41	462	426	56	5	195	56·49	0·731	0·177	0
1954.....	—	—	8	41	426	476	49	—	244	56·52	0·691	0·194	36
1955.....	—	—	—	31	385	519	63	2	541	56·62	0·660	0·096	32
de 1946 à 1952 pas d'observations													

[1]) ‰ des colonnes avec vertèbres soudées

7. Allure de la croissance

(a) Longueur moyenne par rapport à l'âge (Tableau 19).

De 1946 à 1951, on observe d'assez grands écarts saisonniers de la taille moyenne par rapport à l'âge mais leur importance ne dépasse pas certaines limites. Dès 1952, on constate toutefois une nette et constante augmentation générale de cette moyenne.

(b) Valeur de L_1 (Tableau 20).

La valeur moyenne de L_1 des classes d'âge 1950 à 1953 est sensiblement supérieure à celle déterminée pour les classes plus âgées. Ce qui confirmerait que la croissance est devenue plus rapide au cours des dernières années.

8. Vertèbres (Tableau 21 et 22)

Le nombre de vertèbres observées par épine dorsale varie de 52 à 59, mais les nombres extrêmes 52, 53 et 59 sont rarement représentés. Les nombres 56 et 57 se montrent les plus fréquents, mais avec une prédominance du nombre 57. Selon les saisons, 7 à 41‰ des épines dorsales possèdent de vertèbres avec une ou plusieurs soudures; dans les résultats, il est fait abstraction de ces épines.

Dans la région septentrionale, la moyenne vertébrale saisonnière varie de 56·472 (1946) à 56·619 (1951); dans la région centrale, de 56·453 à 56·585 et dans la région méridionale, de 56·492 à 56·619.

En répartissant la moyenne vertébrale d'après les stades de maturité, on constate que les harengs au stades peu développés ont généralement une moyenne vertébrale plus élevée que les harengs à maturité plus avancée.

Tableau 22
Vertèbres: Répartition de la moyenne vertébrale d'après deux groupes de harengs:
1r groupe: harengs aux stades à maturité peu développée
2d groupe: harengs aux stades à maturité plus développée

Années	1r groupe		2d groupe	
	Stades de maturité	Moyenne vertébrale	Stades de maturité	Moyenne vertébrale
1946...	I à III	56·60	IV à VIII–II	56·45
1947...	I à III	56·72	IV à VIII–II	56·47
1948...	I à IV	56·81	V à VIII–II	56·50
1949...	I à III	56·74	IV à VIII–II	56·52
1950...	I à III	56·57	IV à VIII–II	56·49
1951...	I à IV	56·81	V à VIII–II	56·51
1952...	I à IV	56·52	IV à VIII–II	56·52
1953...	I à III	56·62	IV à VIII–II	56·49
1954...	I à IV	56·55	V à VIII–II	56·49
1955...	I à IV	56·57	V à VIII–II	56·54

Tableau 23
Ecailles en carène (K_2): Frequence pour 1000 du nombre d'écailles en carène

Années	Nombre d'écailles en carène									Nombre de harengs	Moyenne	Déviation Standard	Fluctuation probable de la moyenne
	11	12	13	14	15	16	17	18	19				
Région septentrionale													
1946.....	(pas d'observations)												
1947.....	2	12	98	424	374	70	16	4	—	500	14·45	0·908	0·137
1948.....	—	5	110	425	380	70	8	2	—	400	14·43	0·843	0·142
1949.....	—	—	59	337	414	165	23	2	—	689	14·76	0·890	0·114
1950.....	—	7	50	318	439	175	7	—	4	280	14·76	0·890	0·179
1951.....	—	2	58	355	445	115	23	2	—	400	14·69	0·857	0·144
1952.....	—	5	85	360	400	125	25	—	—	200	14·63	0·913	0·218
1953.....	—	4	45	311	479	133	24	4	—	286	14·78	0·863	0·172
1954.....	—	7	40	307	455	168	18	5	—	398	14·81	0·883	0·149
1955.....	(pas d'observations)												
Région centrale													
1946.....	(pas d'observations)												
1947.....	—	2	68	364	448	106	12	—	—	500	14·62	0·815	0·123
1948.....	—	5	137	398	337	107	13	3	—	600	14·46	0·936	0·129
1949.....	—	3	43	289	453	183	22	7	—	629	14·86	0·896	0·121
1950.....	—	—	49	295	466	153	28	7	2	892	14·85	0·911	0·103
1951.....	2	2	63	341	441	135	11	5	—	636	14·69	0·879	0·118
1952.....	—	2	68	326	452	129	20	1	2	895	14·71	0·885	0·100
1953.....	—	2	52	296	458	164	26	1	1	1,023	14·82	0·885	0·093
1954.....	1	2	51	344	428	150	23	1	—	789	14·74	0·875	0·105
1955.....	—	—	61	317	417	162	39	2	2	611	14·81	0·945	0·129
Région méridionale													
1953.....	—	—	55	293	468	169	15	—	—	201	14·80	0·838	0·199
1954.....	—	—	20	323	490	159	8	—	—	251	14·81	0·747	0·159
1955.....	—	2	52	304	476	144	18	2	2	555	14·78	0·865	0·125

de 1946 à 1952 pas d'observations

Cette constatation nous a amené à scinder les harengs en deux groupes: le 1r groupe étant constitué par des harengs aux stades de maturité I à III et le 2d groupe par des harengs aux stades de maturité V à VIII—II. Quant aux harengs au stade de maturité IV, ils sont incorporés au groupe dont ils se rapprochent le plus par leur moyenne vertébrale. Ainsi on a observé que la moyenne vertébrale du 1r groupe, à une exception près, est toujours sensiblement supérieure à celle du 2d groupe (Tableau 22).

La signification de ce décalage n'est pas encore clairement définie, mais il est possible qu'il s'explique par la présence d'une proportion assez importante de Harengs de Printemps dans le 1r groupe, alors que le 2d serait constitué exclusivement par des Harengs d'Automne.

A noter que, dans les régions centrale et méridionale, les moyennes vertébrales des deux groupes se rapprochent beaucoup, ce qui pourrait signifier que les Harengs de Printemps ne s'aventurent pas très loin dans la Mer du Nord.

9. Ecailles en carène, K_2 (Tableau 23)

Le nombre d'écailles en carène varie de 11 à 19. Les nombres extrêmes 11, 12 et 19 sont rarement représentés.

Dans la région septentrionale, les moyennes saisonnières de K_2 varient de 14·43 (1948) à 14·81 (1954); dans la région centrale, de 14·46 (1948) à 14·86 (1949) et dans la région méridionale, de 14·78 (1955) à 14·81 (1954).

Tableau 24
Contenu stomacal: Fréquence pour 1000 des estomacs avec contenu

Années	Régions		
	Septentrionale	Centrale	Meridionale
	Estomacs avec contenu		
1946.....	58	261	?
1947.....	234	192	?
1948.....	105	278	?
1949.....	17	22	?
1950.....	232	266	?
1951.....	135	42	?
1952.....	160	67	?
1953.....	57	58	0
1954.....	147	49	4
1955.....	?	10	0

10. Contenu stomacal (Tableau 24)

La nourriture observée dans les estomacs était, en majeure partie, constituée par des débris de copépodes et dans une moindre mesure de schizopodes.

Dans la région septentrionale, on rencontre, selon les saisons, 17‰ (1949) à 232‰ (1950) d'estomacs avec de la nourriture; dans la région centrale: 10‰ (1955) à 278‰ (1948), et dans la région méridionale, rarement.

25.

Considérations sur les Harengs du Sud de la Mer du Nord et de la Manche Orientale*) (Observations faites de 1945 à 1956)

Par J. Ancellin

Résumé

La présente étude concerne les harengs du sud de la Mer du Nord et de la Manche Orientale qui font chaque hiver, du début de novembre à la fin de février, l'objet de la pêche boulonnaise et dont les concentrations intéressent un secteur géographique s'étendant principalement depuis les Bancs des Flandres jusqu'à la région située au large des côtes des départements de la Somme et de la Seine-Inférieure.

Les caractères biométriques des harengs du sud de la Mer du Nord et de la Manche Orientale n'ont pas subi de modifications par rapport à la période d'avant la guerre.

On peut reconnaître un groupement des harengs du sud de la Mer du Nord ("Downs Herring") à moyenne vertébrale de 56·5 à 56·6 et un groupement des harengs de la Manche Orientale à moyenne vertébrale de 56·6 à 56·7. Ces deux groupements représenteraient des termes de passage entre la race des harengs de la Mer du Nord "Bank Herring" (m.v. = 56·5) et la race des harengs de la Manche (m.v. = 56·7).

Des échanges doivent se produire de part et d'autre du Pas de Calais entre ces deux groupements et de même on peut estimer, d'après les résultats des marquages, que l'aire de répartition des "Downs Herring" ne se limite pas au sud de la Mer du Nord: elle s'étendrait pendant une partie de l'année vers le centre de la Mer du Nord et les détroits danois.

Les lieux de ponte des harengs du sud de la Mer du Nord et de la Manche Orientale se trouvent principalement sur les Bancs des Flandres (novembre) et au large de Dieppe (décembre).

Les rassemblements de ponte sur les Bancs des Flandres se sont produits jusqu'à ces dernières années dans un secteur bien délimité (sud du Sandettié), à époque fixe; ils n'ont pas paru influencés par d'appréciables modifications de la salinité.

Les lieux d'alevinage des harengs pondus dans le sud de la Mer du Nord se situeraient au large des côtes hollandaises, allemandes et danoises.

Dans l'état actuel de nos connaissances, il parait difficile de se prononcer sur les véritables causes qui sont à l'origine des changements intervenus depuis quelques années dans le stock des harengs du sud de la Mer du Nord et de la Manche Orientale. Ces changements consistent notamment en une modification de la composition du stock par suite d'une importance beaucoup plus grande de la classe des harengs de 3 ans, une diminution des vieilles classes et une augmentation de la taille par âge.

Il semble qu'on doive, pour le moment, se borner à des hypothèses pour expliquer ces phénomènes et dans de précédentes communications nous avions indiqué qu'il pouvait s'agir d'une influence de la pêche, d'une influence du milieu, ou peut-être des deux.

De récents travaux étrangers viennent développer soit l'hypothèse de modifications d'ordre biologique (maturité sexuelle plus précoce, par exemple, s'associant au changement de recrutement dont nous avions donné un premier aperçu l'année dernière) éventuellement liées à l'influence du milieu, soit l'hypothèse d'une influence de la pêche pouvant être conjuguée à des phénomènes provenant de changements naturels du milieu.

*) Le texte intégral de cette étude dont nous donnons ici un résumé est destiné à être publié dans la revue *Science et Pêche* (Bulletin d'Information de l'Institut Scientifique et Technique des Pêches Maritimes, Paris).